SCIENTIFIC AGRICULTURE

Volume 24 MAY, 1944 No. 9

SOIL-PLANT RELATIONSHIPS AND VERTICAL ZONATION IN THE SOUTHERN INTERIOR OF BRITISH COLUMBIA[1]

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[Received for publication January 17, 1944]

The broad conception of climate is that progressive series of changes in moisture and temperature conditions occur at different latitudes. These differences produce wide climatic zones with which are associated the main soil and plant formations.

In the southern interior of British Columbia this condition is modified materially by the mountainous nature of the country. A wide variety of climates is produced in comparatively small areas due to the effect of mountain passes, peaks and valleys upon prevailing winds, and of elevation and exposure on temperature and moisture conditions. The net result is that the distribution and extent of soil and vegetation zones is more dependent upon topography than upon latitude.

Because of the roughness of topography and in some cases unfavorable climate, the bulk of the interior region is suited for forestry and grazing rather than for cultivated agriculture. The purpose of the present study was to obtain a better understanding of zonal soil-plant relationships in the area, with particular regard to the application of such information to range utilization. The data presented herein were obtained mainly by means of a soil-plant survey conducted on a section of country known as the Tranquille Range.

The Tranquille Range is situated near the town of Kamloops, (see Figure 1) in the southern interior of British Columbia. Climate and topography are typical for this section of the Province. The lowest elevation is 1,100 feet above sea level, in the bottom of the Thompson River valley. From this point there is a fairly steady increase in altitude to the height of land at 6,100 feet. The general exposure is southerly, although isolated knolls, rocky escarpments, and deep ravines provide an interesting variety of exposures.

The soil covering the entire area is a stony, sandy loam glacial till. There are no significant differences in texture, and the soil "skeleton" is remarkably uniform. The morphological changes in the profile and the vegetation changes are consequently ascribed to climatic differences.

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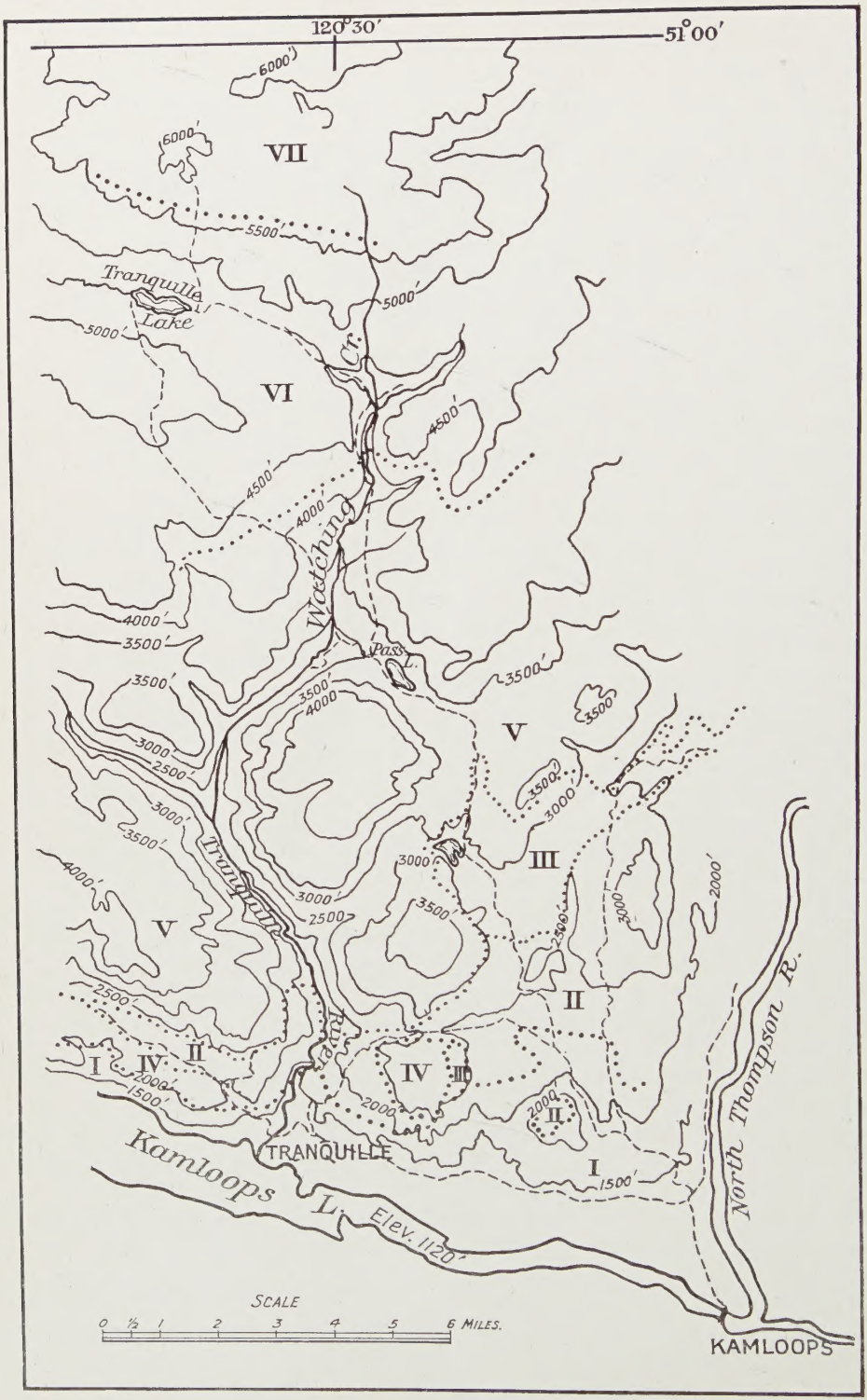

FIGURE 1. *(see opposite page).* Map of part of the Tranquille Range, British Columbia.

Ascending from the lowest elevation there are six distinctive profiles which correspond to the Brown Earth, Dark Brown Earth, Black Earth and three Podsol sub-zones. Associated with each soil type is a corresponding plant community and these are described as Lower, Middle and Upper Grasslands, Montane, Subalpine and Upper Subalpine Forests. The transition from arid grassland to subalpine forest occurs within a horizontal distance of about 30 miles and a vertical distance of 5,000 feet.

The discussion deals in some detail with the succession of changes in soils and vegetation under a vertical distribution of zones, and to a lesser extent with soil-plant relationships within each zone.

REVIEW OF LITERATURE

The relationship between zonal soil and vegetation types is mentioned in most treatises on plant ecology or pedology. There are few references, however, dealing with this subject in any but general terms. Weaver (23), de Sigmond (17), and Thornthwaite (19) deal with vegetation, soil and climate respectively, and discuss interrelationships from their own points of view.

A distinction between vertical and horizontal zonation of soils was recognized in 1899. Dokutschajeff, as quoted by Glinka (9), described vertical soil zones of the Caucasus mountains. Joffe (11), summarizes much of the more recent European literature on soils and vegetation of mountainous regions.

In North America, studies of soil and plant zonation have been confined chiefly to the broad horizontal zones of the central part of the continent. In the mountainous regions of the West, the effects of altitude and exposure on the distribution of plant species and communities have been noted by numerous investigators. In few cases, however, has any attempt been made to determine the nature of the soil types occurring under these same conditions, or the relationship existing between soil and vegetation types.

The only reference the authors have found dealing with a similar study is by Thorp (20). He described a series of six soil zones at various elevations in the Big Horn Mountains of Wyoming and observed a distinctive plant community associated with each. These included desert vegetation, four types of grassland, and one of coniferous forest. The description of plant types is much less complete than that of the soil profiles. Daubenmire (5) has described three grassland zones, in southeastern Washington, and found these associated with three distinct soil series. The same

Legend for Figure 1 (*see opposite page*).

Contour interval	500 feet.	Savanna (Ponderosa pine)	IV
Roads and trails	- - - - - - -		
Zonal boundaries	.....	Lower Podsol Montane Forest	V
Brown Earth Lower Grassland	I	Middle Podsol Subalpine Forest	VI
Dark Brown Earth Middle Grassland	II	Upper Podsol Upper Subalpine Forest	VII
Black Earth Upper Grassland	III		

author (6) has recently reviewed vegetational zonation in the Rocky Mountain region, but soil relationships are given only brief mention. Pearson (13) has investigated the relation of forest types to climate and soil in the southwestern United States.[4]

CLIMATIC DATA

The southern interior of British Columbia, lying between the Coast Range to the west and the Selkirk Mountains to the east, is described generally as a region of low precipitation and high summer temperatures. Since the official weather stations are located mainly in the valley bottoms, their records are of limited value in revealing the variations of climate at different altitudes.

The data used in the following discussion were obtained mainly on the Tranquille Range area from instruments established at typical sites in the various soil-plant zones during the period 1938 to 1940 inclusive. Records of precipitation and temperature extending over a much longer period were available from the Tranquille Sanitorium which is located at the lower edge of the study area, in the Lower Grassland-Brown Earth Zone.

Evaporation was measured by means of spherical Livingston atmometers set at 12 inches above ground level. Records of soil temperature near the surface were obtained by the use of thermographs. Measurements at a depth of 12 inches were made with mercury thermometers suspended in iron pipes driven into the ground as described by Bates and Zon (1).

Precipitation and Evaporation

The 3-year averages of monthly precipitation during the growing season at the various stations are presented in Table 1. The monthly distribution

TABLE 1.—AVERAGE MONTHLY PRECIPITATION AT DIFFERENT ALTITUDES, TRANQUILLE RANGE, 1938 TO 1940 INCLUSIVE

Soil Plant Zone	Altitude	Precipitation						
		April	May	June	July	Aug.	Sept.	Total
	ft.	in.	in.	in.	in.	in.	in.	in.
Brown Earth Lower Grassland	1400	0.32	0.67	1.44	0.57	0.66	0.59	4.25
Dark Brown Earth Middle Grassland	2300	0.41	0.97	1.70	0.78	0.97	0.72	5.55
Black Earth Upper Grassland	2850	0.45	1.30	1.96	1.08	1.04	0.83	6.66
Lower Podsol Montane Forest	3300	0.61	1.44	2.12	1.23	1.18	1.12	7.70

of rainfall in each zone corresponded to that of the southern interior of British Columbia generally, with minimum and maximum amounts falling

[4] Since completion of this manuscript, a paper by Martin and Fletcher (26) dealing with vertical zonation in southern Arizona has come to hand. Their study deals mainly with soils and presents detailed data on the physical, chemical and micro-biological characteristics of several zonal groups. The results of this Arizona study are in general agreement with those obtained in the soil-plant survey of the Tranquille Range.

in April and June respectively. Between zones there was a steady increase in precipitation with increasing altitude.

Records from comparable stations indicate that these data are reasonably representative of long-term trends. The 31-year average April to September rainfall at Tranquille is 4.15 inches, while at Knouff Lake, in the Montane forest zone (altitude 3750 feet) it is 7.05 inches.

Evaporation was recorded for portions of two seasons only but the differences obtained between zones seemed great enough to warrant presentation of the data. In Table 2, the average weekly evaporation in each zone during May and June is presented along with the average precipitation for the same period.

TABLE 2.—EVAPORATION, PRECIPITATION AND THE P/E RATIO AT DIFFERENT ALTITUDES ON THE TRANQUILLE RANGE, MAY AND JUNE, 1939–1940

Soil plant zone	Altitude	Weekly average		
		Evaporation	Precipitation	P/E ratio
	ft.	cc.	in.	
Brown Earth Lower Grassland	1400	405	0.26	6.4
Dark Brown Earth Middle Grassland	2300	330	0.33	10.0
Black Earth Upper Grassland	2850	205	0.41	20.0
Lower Podsol Montane Forest	3300	150	0.43	28.7

The P/E ratio was calculated according to the method used by Livingston and Shreve (12). Precipitation in inches was divided by evaporation in cubic centimetres and the product multiplied by 10,000 to give a figure of reasonable size. It will be noted that differences in evaporation between the various zones were greater relatively than the differences in precipitation. This is emphasized by the P/E ratio which shows considerable variation in moisture conditions with changes of only a few hundred feet in elevation.

Air and Soil Temperatures

Data on air temperature were obtained during two seasons in two zones. The data are summarized in Table 3. The mean difference for the 4 months was 9.3° F., or almost 5 degrees per thousand feet of altitude.

TABLE 3.—MEAN MONTHLY MAXIMUM AND MINIMUM AIR TEMPERATURES, TRANQUILLE RANGE. AVERAGE FOR 1938 AND 1939

Soil plant zone	June		July		Aug.		Sept.		Average		Mean
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	
	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.
Brown Earth Lower Grassland	52	72	58	83	47	84	53	72	52.5	77.7	65.1
Lower Podsol Montane Forest	41	62	45	74	43	78	38	65	41.8	69.8	55.8

Daily and hourly fluctuations in soil temperature were found to be slight at a depth of 12 inches, hence individual weekly readings were considered to be reliable for purposes of zonal comparison. Data obtained in four soil-plant zones are summarized in Table 4.

TABLE 4.—SOIL TEMPERATURES AT 12-INCH DEPTH IN VARIOUS ZONES OF THE TRANQUILLE RANGE, MAY TO SEPTEMBER, 1940

Soil plant zone	Altitude	Soil temperatures		
		High max.	Low min.	Seasonal mean
	ft.	°F.	°F.	°F.
Brown Earth Zone Lower Grassland	1400	76	48	66
Dark Brown Earth Middle Grassland	2300	73	45	62
Black Earth Upper Grassland	2850	66	40	55.5
Lower Podsol Montane Forest	3300	58	38	51

The differences between the sites, while not great, were consistent throughout the period of study.

Soil temperatures close to the surface varied more widely than those at a 12-inch depth. The data obtained in two grassland zones are summarized in Table 5.

TABLE 5.—SOIL TEMPERATURES AT 3-INCH DEPTH IN TWO ZONES OF THE TRANQUILLE RANGE, MAY TO JUNE, 1940

Soil plant zone	Altitude	Soil temperatures		
		Mean max.	Mean min.	Mean
		°F.	°F.	°F.
Brown Earth Lower Grassland	1400	76.5	59.5	68.0
Dark Brown Earth Middle Grassland	2300	63.5	44.5	54.0

The data from this and the preceding table indicate that soil temperatures decreased fairly regularly with increased altitude, the greatest differences occurring in the surface soils of the different zones.

The influence of altitude on temperature, and thus on development of vegetation and soils, is reflected in the data for length of the frost-free period. During the years 1938 and 1939 for which data are available, the average frost-free period was 178 days in the Lower Grassland zone and 116 days in the Montane forest zone. Comparable information was not obtained for the other zones.

Discussion of Climatic Data

The data indicate that, in the zones for which records were obtained, precipitation increased while evaporation, mean temperatures, and the length of the frost-free period decreased with increasing altitude. These results are in general accord with those obtained by numerous investigators in the Rocky Mountain region and elsewhere.

Although climatic data were not obtained for the zones above the Montane, observations of length of growing season, depth of snow cover, and soil moisture conditions indicated that the trends found at lower altitudes tended to persist at higher levels. That such is the case with temperature and length of frost-free season seems likely from the results obtained by other workers in comparable regions. Price and Evans (14) found that in the Wasatch Mountains of Utah, mean air and soil temperatures and the length of the frost-free season decreased steadily from the lowest to highest (spruce-fir) zone studied. Daubenmire (6) states that mean air temperatures decrease on the average about 3 degrees Fahrenheit per thousand feet in the Rocky Mountain region.

On the other hand it has been found that moisture conditions often do not become progressively more favorable up to the highest altitudes. Daubenmire (6) reviewing climatic conditions affecting Rocky Mountain vegetation, points out that maximum precipitation frequently occurs well below the tops of mountain ranges. Precipitation usually reaches a maximum in either the spruce-fir (Subalpine), or Douglas fir (Montane) zone. Similarly, the decrease in evaporation with increasing altitude tends to be checked near the upper timber line due to the influence of decreased atmospheric pressure and increased insolation and wind velocity. Most studies in the Rocky Mountain region (6, 13, 25) have shown evaporation to be at a minimum in either the spruce-fir or Douglas fir zones and to increase in the zones above and below.

Taking both local observations and the results of studies in comparable areas into account, it appears probable that the P/E ratio in the Tranquille area increases to a maximum in the Subalpine (spruce-fir) zone and decreases in the Upper Subalpine type above.

METHODS OF STUDY

Preliminary inspection of larger units was followed by more intensive study of a considerable number of sample areas. Each site represented either conditions typical of large areas, or interesting variations of these conditions; 160 of these sample plots were established on the Tranquille range.

At each site, the location was determined and mapped, and the topographical features noted and described. A soil pit was dug, the profile studied and described, and samples obtained for subsequent determinations of pH, texture, etc.

The plant cover at each site was described, and the constituent species rated for abundance, height, vigour, etc. For plant studies, the area occupied by each site was taken as 100 square metres, (4 square rods). This unit was found to be one which could be studied conveniently by the methods used, and was large enough to give a representative list of species.

Estimates of the various characters of the plant cover were made according to numerical scales. The scale used for abundance was as follows:

5 — Dominant, very abundant.
4 — Sub-dominant, abundant.
3 — Common.
2 — Occurring, but not common.
1 — Rare.

A collection was made of virtually all plant species encountered in the study. The identifications of grasses were checked by Dr. J. R. Swallen, United States Dept. of Agriculture, Washington, D.C., while Dr. H. A. Senn, Division of Botany, Science Service, Ottawa, checked those of other flowering plants. Miss Frances Wynne, Botany Dept., University of Michigan, determined the mosses, and Mrs. Lucy C. Raup, Jamaica Plain, Massachusetts, identified the lichens.

Following the method of Braun-Blanquet (2), a table was prepared for each zone in which were listed the species found at each site, together with their abundance, life-forms, etc. From this table was derived the *average abundance* and *frequency* (percentage occurrence) of each species. By comparison of the summaries for the different zones, the *characteristic species* for each were determined. The latter were forms confined largely or entirely to one zone.

As the work progressed, zonal boundaries were recognized and mapped. In most cases it was found that the boundaries of the major soil and plant types corresponded closely. Additional study was given to areas in which discrepancies occurred.

Near the close of the survey, one typical site in each zone was revisited, and samples from the various soil horizons obtained for chemical study.

In addition to the survey of the Tranquille area, short excursions were made to representative areas in adjacent parts of the Interior. A few sites were studied at each of these localities, in order to test the results obtained at Tranquille.

The soil-plant survey was made during the season of 1938. In the following two years, further plant studies were made at a number of sites in the grassland zones. Areas possessing well developed soil profiles and vegetation approximating the climax type were chosen for this work. At each site several meter quadrats were established and their cover measured by the area-list method. These plots were clipped later to determine the yield of forage.

VEGETATION OF THE GRASSLAND ZONES

Three grassland communities occur in association with the three zonal types of grassland soils. On account of their vertical distribution, these plant associations are designated in this study as the Lower, Middle, and Upper Grassland zones.

The Lower Grassland belt occurs at elevations of 1100 to about 2300 feet and coincides with the Brown Earth zone. From 2300 to 2800 feet is found the Middle Grassland zone, associated with Dark Brown soils. The Upper Grassland type extends from the upper edge of the Middle

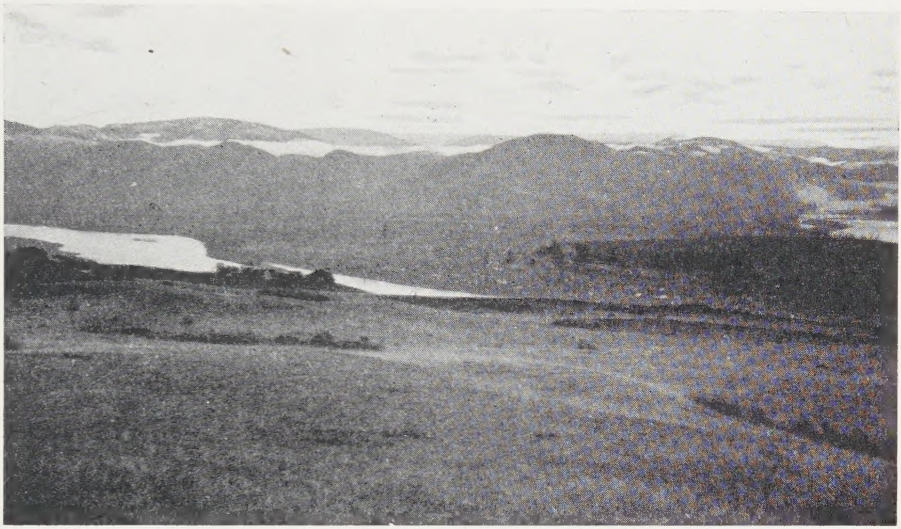

FIGURE 2. General view of Tranquille Range, looking north from south side of Thompson River Valley. Snow still present on Upper Grassland and Forest Zones in March.

FIGURE 3. Upper Grassland zone with Montane forest on higher land in the background. Note clumps of aspen in depressions and intrusion of Douglas fir into grassland on sheltered slopes.

Grasslands to the forest edge at about 3200 feet and coincides with the Black Earth zone.

All three grassland associations are dominated mainly by perennial bunchgrasses, particularly *Agropyron spicatum* (blue-bunch wheatgrass). The whole grass land formation belongs to the Palouse Prairie as described by Weaver (24), Weaver and Clements (23) and others. This is an extensive type characteristic of the Intermountain regions of northern Utah, southern Idaho, eastern Washington and Oregon and southern British Columbia. Daubenmire (5) has reported the presence of three main associations in the Palouse prairies of southeastern Washington and adjacent Idaho. These associations, described as the *Artemisia-Agropryon*, *Agropyron-Poa*, and *Festuca-Agropyron* zones, correspond to a considerable degree with the three grassland types recognized on the Tranquille range.

Botanical Composition

A list of the species occurring commonly on the Tranquille grasslands, together with their relative frequency and abundance is presented in Table 6. These data, based on a study of some 75 sample plots distributed

TABLE 6.—LIST OF SPECIES OCCURRING COMMONLY ON GRASSLAND ZONES OF THE TRANQUILLE RANGE

Scientific name	Popular name	Frequency		
		Lower	Middle	Upper
		%	%	%
Shrubs				
Artemisia tridentata Nutt.	Sagebush	**90**	20	—
Chrysothamnus nauseosus (Pall) Britt.	Rabbit brush	63	45	—
Rosa sp.	Wild rose	—	5	40
Symphoricarpos racemosus Mich.	Snowberry	—	—	20
Grasses and Sedges				
Agropyron spicatum Pursh. var. *inerme* Heller	Bluebunch wheatgrass	**75**	**72**	**63**
Bromus tectorum L.	Downy bromegrass	25	**52**	10
Festuca scabrella Torr.	Rough fescue	—	10	**25**
Koeleria cristata (L) Pers.	Junegrass	16	48	63
Poa pratensis L.	Kentucky bluegrass	—	5	**50**
Poa secunda Presl.	Dwarf bluegrass	**90**	**80**	40
Sporobolus cryptandrus (Torr) A. Gray	Sand dropseed	**63**	15	—
Stipa comata Trin. & Rupr.	Common speargrass	**63**	**55**	15
Stipa columbiana Macoun	Columbia speargrass	—	—	**67**
Carex praegracilis W. Boott	Graceful sedge	—	6	50
Juncus balticus Willd.	Dwarf rush	—	5	40
Forbs*				
Achillea millefolium L.	Yarrow	4	47	75
Antennaria dimorpha T. & G.	Dwarf everlasting	**90**	**95**	60
Antennaria parvifolia Nutt.	Everlasting	—	25	63
Artemisia frigida Willd.	Pasture sage	50	35	5
Astragalus serotinus A. Gray	Poison vetch	—	—	63
Balsamorhiza sagittata Nutt.	Balsam root	24	**53**	25
Delphinium bicolor Nutt.	Dwarf larkspur	—	14	65

* Forbs are non-grasslike, herbaceous plants.

TABLE 6.—LIST OF SPECIES OCCURRING COMMONLY ON GRASSLAND ZONES OF THE TRANQUILLE RANGE—*Concluded*

Scientific name	Popular name	Frequency		
		Lower	Middle	Upper
		%	%	%
Forbs—*Concluded*				
Erigeron compositus Pursh.	Fleabane	—	18	32
Erigeron filifolius (Hook) Nutt.	Fleabane	40	3	—
Erigeron corymbosus Nutt.	Fleabane	5	55	50
Geranium viscosissimum F. & M.	Geranium	—	—	30
Lomatium macrocarpum (Nutt.) C. & R.	Parsley	48	48	10
Lithospermum pilosum Nutt.	Puccoun	—	10	36
Opuntia fragilis Haw.	Cactus	60	20	—
Taraxacum officinale. Weber	Common dandelion	—	5	32
Taraxacum erythrospermum Anderz	Red-fruited dandelion	20	40	40
Zygadenus venenosus Wats.	Death camas	—	5	50

N.B. Frequency figure in bold type indicates dominance of the species in that zone.

over the three zones, indicate the extent to which all three associations are dominated by grasses and composites. Certain genera, such as *Agropyron*, *Stipa*, *Antennaria* and *Artemisia* are particularly well represented, although within each genus the same species do not usually occur in all three zones. For example, *Stipa* is represented by *S. comata* in the Lower and Middle grasslands, and by *S. columbiana* in the Upper zone. The outstanding exception in this regard is *Agropyron spicatum* which occurs abundantly in all three types.

The number of species increases from the lower to the higher zones. Only 15 species were found occurring with a frequency of 10% or more in the Lower Grasslands, as compared to 20 species in the Middle zone and 25 in the Upper Grassland association.

The Lower Grassland zone is dominated by 4 grasses *Agropyron spicatum*, *Poa secunda*, *Stipa comata* and *Sporobolus cryptandrus*, along with 1 shrub, *Artemisia tridentata* and 1 dwarf forb, *Antennaria dimorpha*. These 6 species comprise about 90% of the sparse plant cover. Common plants include 1 shrub, *Chrysothamnus nauseosus*, 1 cactus, *Opuntia fragilis*, and a few herbaceous species, *Artemisia frigida*, *Erigeron filifolius* and *Lomatium macrocarpum*.

The dominants of the Middle Grassland zone include the same species of *Agropyron*, *Poa*, *Stipa*, and *Antennaria* as were listed for the Lower Grasslands. In addition, *Bromus tectorum* is dominant on certain overgrazed areas. Common species include *Chrysothamnus nauseosus*, *Koeleria cristata*, *Balsamorhiza sagittata*, *Achillea millefolium* and *Erigeron corymbosis Artemisia tridentata* is common only on the lower fringes of the zone.

The Upper Grassland association does not exhibit such clear cut dominance of a few species as is found in the lower zones. The principal species are 4 grasses, namely *Agropyron spicatum*, *Festuca scabrella*, *Poa pratensis* and *Stipa columbiana*. In addition, there are several species

which, while not ranking as dominants, are quite abundant. This group comprises a grass *Koeleria cristata*, a sedge *Carex praegracilis*, a dwarf rush *Juncus balticus* and a number of forbs including *Antennaria parvifolia*, *Achillea millefolium*, *Astragalus serotinus*, *Delphinium bicolor*, *Erigeron corymbosus* and *Zygadenus venenosus*.

A conspicuous feature of the zone is the presence of clumps of aspen (*Populus tremuloides*) in shallow depressions and on sheltered slopes. Two shrubs, *Rosa* sp. and *Symphoricarpos racemosa* occur in patches on favored locations.

The three zones differ greatly in the nature of their characteristic plants. Those of the Lower Grasslands are drought-tolerant species of southern origin such as *Artemisia tridentata*, *Erigeron filifolius*, *Opuntia ragilis* and *Sporobolus cryptandrus*. The characteristic species of the Upper Grassland are relatively mesic forms such as *Poa pratensis*, *Stipa columbiana*, *Carex praegracilis*, *Delphinium bicolor*, and *Geranium viscosissimum*.

The Middle Grassland zone contains practically no characteristic species. Absence of the characteristic plants of the other two associations is its main distinguishing feature floristically.

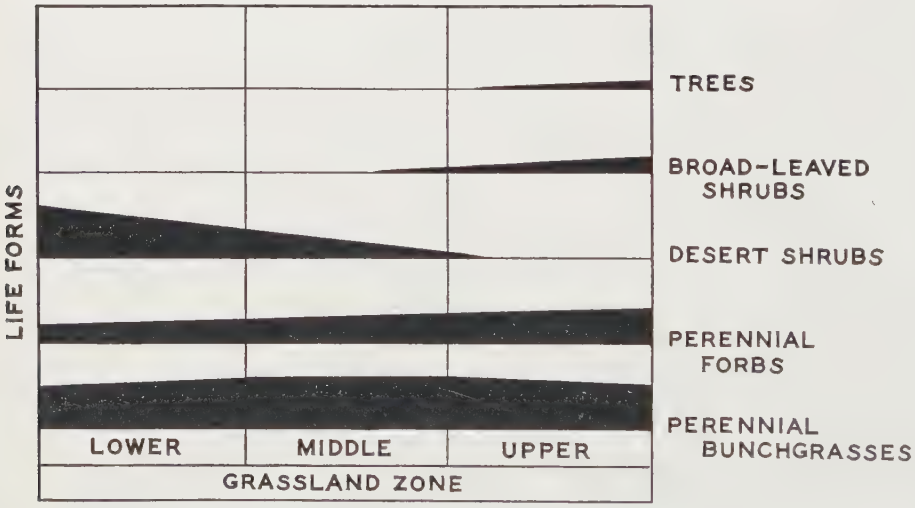

FIGURE 4. Relative Importance of Main Life-forms in grassland zones. Tranquille Range.

Life Forms and Seasonal Growth

The life forms of plants, representing the reaction of the plant body to the environment, constitute valuable indicators of habitat. The nature and relative importance of the principal life forms occurring in the Tranquille grasslands are indicated in Figure 4. Both numbers of species and abundance of individual plants in each class were considered in preparing this figure.

The principal life form is the perennial bunchgrass, well adapted for existence in all three zones, but reaching its maximum abundance in the Middle Grassland type. Rhizomatic grasses are common only in the moister

portions of the Upper Grasslands. The xeric desert shrubs are restricted to the two lower zones and attain most importance in the Lower Grassland association. Broad-leaved shrubs (*Rosa*, etc.) are confined to the moister parts of the Upper Grasslands.

Perennial forbs, while occurring in all three zones, are much more abundant and luxuriant in the Upper Grassland association. Most of the forbs which do occur in the lower zones are either dwarf forms (*Antennaria dimorpha*) or short-season, drought-escaping species (*Balsamorhiza sagittata*, *Lomatium macrocarpum*). Moisture conditions are generally unsuitable for tree growth except in favoured locations in the Upper Grassland zone.

Studies of seasonal growth development over a period of five years revealed marked differences in the three zones. The average date of first growth was March 18 in the Lower, March 27 in the Middle, and April 9 in the Upper Grassland zone. These differences reflect the influence of decreasing soil and air temperatures with increasing altitude. In the Lower Grasslands, the vegetation usually cured and became dormant during July and August, reviving to some extent with the autumn rains. A similar course occurred in the Middle Grassland, with the date of curing averaging a few days later. In the Upper Grassland zone, moisture conditions were sufficiently favorable to maintain much of the vegetation in a green state throughout the summer in average years.

Structure and Productivity

The plant cover of the grasslands becomes progressively denser and more productive with increasing altitude. A summary of data on basal cover and yield from 45 meter quadrats established on representative areas of relatively climax vegetation in the three zones is presented in Table 7.

TABLE 7.—DENSITY AND YIELD OF CLIMAX VEGETATION IN THE GRASSLAND ZONE, 1939

Zone	Density	Yield
	%	lb. per acre
Lower Grassland	7	370
Middle Grassland	11	560
Upper Grassland	16	1200

It will be noted that the increase in yield from the lowest to highest zone is greater than that in density, indicating that taller growth is a factor affecting productivity.

Because of the relatively open nature of the plant cover, stratification is generally poorly developed in the two lower zones. In the Upper Grassland there are two fairly well marked strata, an upper layer of grasses and taller forbs and a lower layer of shorter forbs.

Successional Relationships

It was evident during the course of the soil-plant survey that the plant cover of the Tranquille grasslands had been disturbed greatly by overgrazing. Subsequent study of lightly grazed sites yielded considerable information regarding the nature of the climax vegetation in each zone.

FIGURE 5. Typical open cover of bluebunch wheatgrass on meter quadrat located in climax vegetation of the Lower Grassland zone.

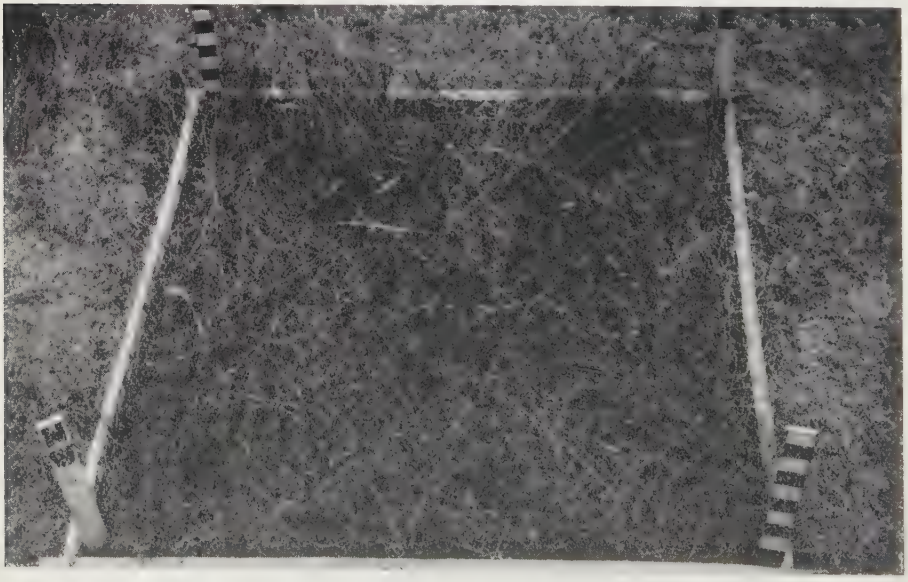

FIGURE 6. Heavy sod, composed mainly of Kentucky bluegrass, in meter quadrat on deep soil in Upper Grassland zone.

In the Lower Grasslands, the climax vegetation appears to consist mainly of perennial bunchgrasses, particularly *Agropyron spicatum* which forms practically pure stands on many undisturbed sites. In the Middle Grassland type, these same bunchgrasses are clearly dominant.

In the Upper Grassland area, undisturbed sites were very few and it was more difficult to ascertain the nature of the original plant cover. Apparently bunchgrasses, especially *Agropyron spicatum* and *Festuca scabrella* are the principal climax species, but certain other grasses and many forbs apparently occurred in considerable abundance in the original vegetation.

VEGETATION OF THE FOREST ZONES

Three forest communities are associated with the three types of podsols. These associations are designated as the Montane, Subalpine and Upper Subalpine forests and coincide with the Lower, Middle and Upper Podsols respectively. The Montane forest occurs immediately above the Upper Grassland zone, at altitudes of 3200 to 4000 feet and has Douglas fir (*Pseudotsuga taxifolia*) as its main climax dominant. Above this zone, from 4000 to 5800 feet occurs a forest type whose climax dominants are Engelmann spruce (*Picea Engelmanni*) and subalpine fir (*Abies lasiocarpa*). From 5800 to the height of land at 6100 feet is the Upper Subalpine type, characterized by many of the same dominants as those of the Subalpine, but distinguished by differences in tree density and growth as well as by the presence of extensive treeless openings.

The Montane forest belongs to one of the major Rocky Mountain plant formations, the Petran Montane type of Weaver and Clements (22) or the Douglas Fir zone of other authors (6). Similarly the Subalpine type corresponds to the Petran Subalpine formation (22) or Spruce-Fir zone (6). The Upper Subalpine type of this study probably represents a transition between the Subalpine and Alpine zones. The occurrence of somewhat similar vegetation along the upper edge of the Subalpine forest has been reported by several investigators (6, 7) in the Rocky Mountain region. The altitude of the Tranquille area is not sufficient to allow the development of the Alpine zone which does not occur below 7000 feet in this vicinity.

Botanical Composition

A list of the species occurring commonly, along with their relative frequencies in the different forest zones is presented in Table 8. Floristic-

TABLE 8.—LIST OF SPECIES OCCURRING COMMONLY ON FOREST SITES, TRANQUILLE RANGE

Scientific name	Popular name	Frequency		
		Montane.	Sub-Alp.	Upper Sub-Alp.
Trees		%	%	%
Abies lasiocarpa (Hook) Nutt.	Subalpine fir	—	**60**	40
Picea Engelmanni Parry.	Engelmann spruce	5	**70**	**80**
Pinus ponderosa Dougl.	Ponderosa pine	**20**	—	—
Pinus contorta Dougl. var. *latifolia* Engelm.	Lodgepole pine	**80**	**90**	5
Pseudotsuga taxifolia (Lamb) Brit.	Douglas fir	**65**	10	—
Populus tremuloides Michx.	Aspen, poplar	**85**	20	—
Salix spp.	Willow	65	40	50

TABLE 8.—LIST OF SPECIES OCCURRING COMMONLY ON FOREST SITES, TRANQUILLE RANGE —*Concluded*

Scientific name	Popular name	Frequency		
		Montane	Sub-Alp.	Upper Sub-Alp.
		%	%	%
Shrubs				
Amelanchier alnifolia Nutt.	Saskatoon	35	—	—
Lonicera involucrata Banks	Twinberry	5	40	5
Pachystima myrsinites Raf.	False box	10	**60**	—
Rosa spp.	Rose	**90**	20	—
Sheperdia canadensis (L) Nutt.	Sopolallie	**90**	30	—
Spiraea lucida Dougl.	Spiraea	60	10	—
Vaccinium membranaceum Dougl.	Huckleberry	15	**80**	10
Grasses and Sedges				
Calamagrostis rubescens Buckl.	Pinegrass	**100**	30	—
Danthonia intermedia Vasey	Oatgrass	—	—	**40**
Deschampsia atropurpurea (Wahl) Scheele	Mountain hairgrass	—	5	**65**
Phleum alpinum L.	Alpine timothy	—	—	35
Trisetum spicatum (L) Richter	False oatgrass	—	20	50
Carex concinnoides Mack.	Dwarf sedge	70	70	25
Forbs and Dwarf Shrubs				
Achillea millefolium L.	Yarrow	45	—	—
Antennaria Howellii Greene	Everlasting	35	10	—
Antennaria umbrinella Rydb.	Everlasting	—	—	40
Aster conspicuus Lindl.	Rough aster	95	20	—
Forbs and Dwarf Shrubs (*continued*)				
Arnica cordifolia Hook.	Arnica	80	80	15
Astragalus scrotinus A. Gray	Poison vetch	60	—	—
Castilleja miniata Dougl.	Painted bush	50	5	—
Cornus canadensis L.	Bunchberry	5	60	—
Epilobium angustifolium L.	Fire-weed	15	70	20
Fragaria glauca (Wats.) Rydb.	Strawberry	70	60	20
Hieracium umbellatum L.	Hawkweed	55	—	—
Lathyrus ochroleucus Hook.	Peavine	80	—	—
Lilium parviflorum (Hook.)	Red lily	45	30	—
Linnaea borealis Holtz. var. *americana* (Rehder) Forbes	Twin flower	50	70	—
Pedicularis bracteosa Benth	Lousewort	10	80	80
Sibbaldia procumbens L.	Sibbaldia	—	—	60
Valeriana sitchensis Bong.	Valerian	—	15	55
Vicia americana Muhl.	American vetch	45	—	—
Arctostaphylos uva-ursi. Spreng.	Kinnikinnick	80	10	—
Berberis aquifolium Pursh.	Oregon grape	75	—	—
Vaccinium caespitosum Mich.	Dwarf blueberry	20	10	**80**
Vaccinium scoparium Leiberg.	Blueberry	5	**100**	**45**
Lupinus sp.	Blue lupin	25	80	90
Pyrola secunda L.	Wintergreen	35	70	10
Mosses and Lichens				
Brachythecium spp.	Moss	30	**100**	**80**
Polytrichum juniperum var. *alpestre* B.S.G. Bryol. Eur.	Hairy cap moss	15	**80**	**85**
Hypnum crista-castrensis L.	Feather moss	—	**30**	?
Peltigera canina Willd.	Foliose lichen	25	**80**	**80**
Cladonia fimbriata Fr.	Fruticose lichen	10	**80**	**85**
Cladonia gracilis Willd.	Fruticose lichen			

N.B. Frequency figure in bold type indicates dominance of the species in that zone.

ally, the forest vegetation is characterized by greater variety than are the grasslands. The pine, willow, rose, heath, grass and composite families are well represented. The number of species recorded as occurring with a frequency of 10% or more is 36 for the Montane, 35 for the Subalpine and 25 for the Upper Subalpine zone.

Most species are confined to one or at most two zones, although there are a few plants such as *Carex concinnoides*, *Arnica cordifolia* and *Epilobium angustifolium* which occur in all three associations.

The dominant trees of the Montane zone are Douglas fir, lodgepole pine and aspen. Several species of willow are common. Ponderosa pine occurs on warm dry slopes, mainly in the lower part of the zone. The principal shrubs are *Shepherdia canadensis* and *Rosa* spp., while *Spiraea lucida* occurs commonly. The dominant herb is *Calamagrostis rubescens* (pinegrass) which comprises about half the herbaceous cover. Other important herbs include *Carex concinnoides*, *Arnica cordifolia*, *Aster conspicuus*, *Astragalus serotinus*, *Fragaria glauca* and *Lathyrus ochroleucus*. Two dwarf evergreen shrubby species. *Arctostaphylos uva-ursi* and *Berberis aquifolium* are common. Mosses and lichens are not abundant.

In the Subalpine zone, the dominant trees at present are lodgepole pine, Engelman spruce, and subalpine fir in relative order of abundance. The principal shrubs are *Vaccinium membranaceum*, *Pachystima myrsinites* and *Lonicera involucrata*. The herbaceous cover is relatively sparse and is dominated mainly by a dwarf, blueberry, *Vaccinium scoparium*. Other common species include *Cornus canadensis*, *Fragaria glauca*, *Lupinus* sp., *Pedicularis bracteosa*, *Pyrola secunda* and *Linnaea borealis*. The mosses *Brachythecium* sp. and *Polytrichum juniperum* and the lichens, *Peltigera canina* and *Cladonia* spp. are abundant.

The vegetation of the Upper Subalpine zone consists of forest alternating with treeless openings dominated by herbaceous species. The principal tree in the forested portions is Engelmann spruce, while subalpine fir is less abundant. Lodgepole pine and aspen are rare in this zone. The shrub cover is poorly developed and consists mainly of dwarf willows. *Vaccinium scoparium* dominates in the herb layer, but not to so marked an extent as in the Subalpine zone. *Lupinus* sp., *Pedicularis bracteosa* and *Vaccinium caespitosum* are abundant. The moss and lichen cover is similar to that of the Subalpine association, but not so dense.

The treeless openings of the Upper Subalpine zone are of two types, one dominated mainly by forbs and dwarf shrubs, the other by grasses. In the first type the principal species is *Vaccinium caespitosum*, while *Antennaria umbrinella*, *Pedicularis bracteosa* and *Sibbaldia procumbens* are sub-dominant. The grass or "mountain meadow" type supports a dense turf dominated by *Danthonia intermedia* along with lesser amounts of *Carex spp.*, *Trisetum spicatum*, *Phleum alpinum* and *Sibbaldia procumbens*.

Each of the three zones has a number of characteristic species. Some of the more important of these in the Montane association are Douglas fir, *Spiraea lucida*, *Berberis aquifolium*, *Astragalus serotinus* and *Lathyrus ochroleucus*. Characteristic species of the Subalpine include *Pachystima myrsinites* and *Cornus canadensis*. In the Upper Subalpine characteristic plants include *Danthonia intermedia*, *Deschampsia atropurpurea*, *Vaccinium*

caespitosum and *Sibbaldia procumbens*. If the two divisions of the Subalpine zone be considered as comprising one major type, this would have as additional characteristic species, Engelmann spruce, subalpine fir and *Vaccinium scoparium*.

Life Forms and Seasonal Growth

The forest zones contain a greater variety of life forms than occur in the grasslands. The relative importance of the principal forms in each of the forest types is indicated in Figure 7. The outstanding feature of all three zones is the dominance of evergreen, coniferous trees. This life form is well adapted to the relatively low temperatures, short growing season and moderate precipitation of the higher altitudes of the Tranquille region just as perennial bunchgrasses are adapted to the warmer and drier conditions existing on the lower slopes. The typical form of the dominant conifers is altered considerably in the Upper Subalpine zone where they are relatively shorter with sharply tapering trunks.

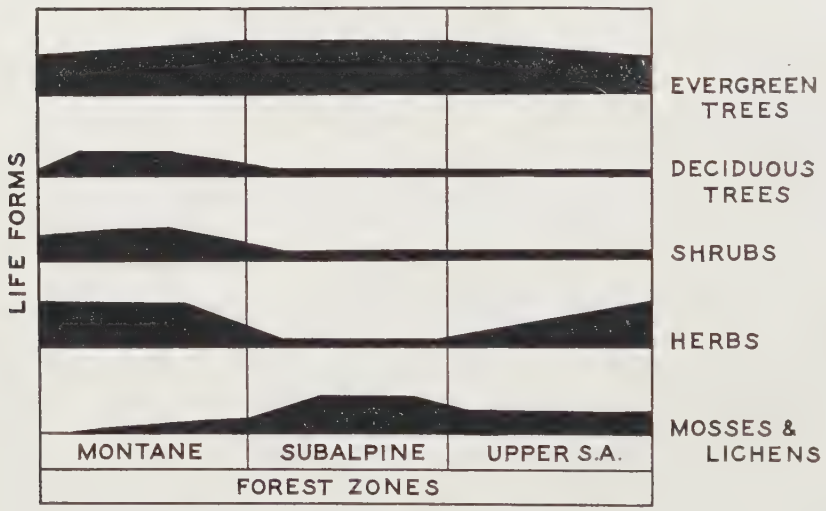

FIGURE 7. Relative Importance of Main Life-forms in forest zones of the Tranquille Range.

Shrubs flourish mainly in the Montane zone, where the tree cover is fairly open. In the Upper Subalpine the shrub form is assumed by several species of willow.

Grasses and other herbs grow well in both the Montane and Upper Subalpine associations, but are less vigorous and common in the dense shade of the Subalpine forest. Mosses and lichens thrive on the cool, moist and acid forest floor of this latter zone. Only the more xeric types of moss and lichen occur in the Montane association.

The period of growth starts later in each successively higher zone. Over a 4-year period the average date of first growth for the dominant species of the forest floor was April 22 for the Montane zone, May 12 for the Subalpine, and a week or more later for the Upper Subalpine. These

observations are in general accord with those obtained in similar zones farther south. Costello and Price (4) found that in the Wasatch Mountains of Utah the growing season begins 10 to 14 days later with each increase of a thousand feet in altitude.

Structure

The density of the forest increases from the relatively open stands formed by mature Douglas fir in the Montane zone to denser covers of spruce and fir in the Subalpine. In the Upper Subalpine the stands become thinner and are broken by numerous treeless tracts of considerable extent.

The density of the shrub cover decreases from the Montane to the Subalpine and shows little increase in the Upper Subalpine. Herbaceous vegetation is most abundant in the Montane and least in the Subalpine. With mosses and lichens the reverse is true.

Successional Relationships

The vegetation of all three forest zones has been subjected to repeated fires which have altered greatly the composition of the tree cover. In the Montane zone, many stands of Douglas fir have been destroyed and replaced by lodgepole pine and aspen. There is good evidence that with protection from fire, the fir will become dominant again by shading out the less tolerant pine and aspen. Since Douglas fir is a thick-barked species, many of the older individuals have withstood the ravages of fire and remained to serve as seed trees for new generations.

In the Subalpine zone, destruction of the thin-barked dominants, Engelmann spruce and subalpine fir, has been more complete. Over considerable areas in the Tranquille forest scarcely a spruce or fir occurs at present, the tree cover consisting almost entirely of lodgepole pine. Aspen is not nearly so abundant as in burned areas in the Montane zone.

Fires have occurred in the Upper Subalpine, although apparently not so often as in the lower forest zones. Lodgepole pine and aspen are rare in this association, and burned areas appear to be revegetated directly, although slowly, by the climax spruce and fir.

The composition of the shrub, herbaceous, and moss layers in the forest zones does not appear to have been altered greatly by the changes in tree cover resulting from fire. In some cases, as under aspen in the Montane zone, the herbaceous cover is denser and more luxuriant than in stands of climax timber, but the botanical composition is not changed significantly. This feature is of considerable importance in the recognition of zonal types in cases where the climax tree cover has been destroyed by fire and replaced by species such as lodgepole pine which are abundant in more than one zone.

The two types of treeless opening in the Upper Subalpine differ in successional status. The type dominated by forbs contains numerous remnants of charred wood, indicating previous occupation by forest. The presence of saplings appears to mark the beginning of re-occupation by forest. Restoration of tree stands must be very slow in this zone, for fires are not known to have occurred in the area for at least 20 years. The

grassland type of opening shows no signs of former forest occupation or present invasion of trees. Presumably it is a climax type under present climatic and soil conditions.

GRASSLAND SOILS

Profile descriptions

Brown Earths are to be found at the lowest elevation and they extend from 1100 to about 2300 feet. They are succeeded by Dark Brown Earths which occur as a belt between 2300 and 2800 feet, above which Black Earths carry through to the beginning of the forest soils. The upper limit of the Black Earths is about 3200 feet elevation.

The succession of soil zones follows the normal pattern, though as noted later, interesting variations occur with changing topography and exposure. The following descriptions are of profiles occurring in these three zones.

Brown Earth

Horizon	Depth	
A_1	0–10″	Brown loam, soft indefinite crumb structure, porous.
B_1	10–16″	Grey brown loam, hard and massive though softening slightly with depth, permeability is restricted. Lime concretions and pockets of gypsum crystals occur.
B_2	16–19″	Grey brown to bluish grey sandy loam, a partially weathered fragmentary glacial till, heavily impregnated with lime.
C	19″	Grey sandy loam, a strongly cemented glacial till, impervious to roots and moisture. No visible lime.

Dark Brown Earth

Horizon	Depth	
A_1	0–8″	Dark brown sandy loam, soft indefinite crumb structure, porous.
B_1	8–28″	Drab brown sandy loam, very dense, tough and massive with porosity greatly restricted. It is impregnated with streaks and specks of lime.
B_2	28–31″	Grey brown sandy loam, a partially weathered glacial till containing a heavy accumulation of lime.
C	31″	Grey brown sandy loam, a strongly cemented glacial till completely impervious.

Black Earth

Horizon	Depth	
A_1	0–8″	Very dark brown to black sandy loam, with a light floury texture.
B_1	8–18″	Dark brown sandy loam, dense and compact but not hard. Porosity is slightly restricted, lime specks occur.
B_2	18–24″	Grey brown sandy loam, a partially weathered glacial till with a heavy accumulation of lime.
C	24″	Grey brown sandy loam, a strongly cemented glacial till, containing no visible lime and impervious.

All profiles contain basaltic sub-angular gravel and stone.

Morphological Features

The most conspicuous features common to all three profiles are, *(a)* a shallow A_1 horizon, *(b)* a dense tough B_1 horizon, *(c)* a strong accumulation of free lime close to the surface, and *(d)* a strongly cemented, impervious C horizon. Each of these features plays a part in the development of the profile as a whole.

The depth of the A_1 horizon seldom exceeds 10 inches, even in the Black Earth zone. The shallowest soils are to be found on the crests of ridges, and the depth increases toward the toe of slopes. The average depth of the A horizon over the Tranquille Range is less than the average for relatively level sites where normal profile development should be expected to occur.

The shallowness is probably due to surface creep and sheet erosion. Sheet erosion was indicated by a piling up of soil material against the upper side of the crown of grass plants. Gully erosion occurs, but not to a marked degree. Since the entire area is a rolling hillside it is not surprising that shallow soils through erosion are a characteristic of the range.

A dense tough B_1 horizon is common to all zones but is most strongly developed in the Dark Brown Earth profiles. It is a feature of degraded profiles and has led the writers to suspect a solonetz development.

Mechanical analysis reveals that there has been a movement of clay for there is an accumulation of about 4% in the B_1 horizon of the Dark Brown Earths. The Brown and Black Earths show no such accumulation. The chemical analysis in Table 9 shows no movement of sesquioxides, however.

The pH of the B horizons of the Brown and Dark Brown Earths is high, but is not accompanied by any accumulation of sodium. Exchangeable sodium, shown in Table 10 does not exceed 1%. There is a high concentration of exchangeable magnesium, however, in the Brown and Dark Brown Earths and it is possible that this feature accounts for the dispersed, solonetz-like structure of the B_1 horizon in each zone.

The restricted porosity of the B_1 horizon in all three zones is an important factor in increasing the proportion of surface run-off water, which in turn accentuates sheet erosion.

An accumulation of calcium occurs in all three profiles. The depth varies from 10 inches in the Brown Earths to about 20 inches in the Black Earths. The accumulation of free lime, as shown by CO_2 analysis in Table 9 indicates a maximum concentration in the B_1 horizon of the Brown Earths, B_2 of the Dark Brown Earths and C horizon in the Black Earths.

The whole of the Tranquille Range area including both grassland and forest, is underlain by an extensive, strongly cemented glacial till, concrete-like in consistence. Similar tills are characteristic of several British Columbia series and also occur in Washington (18) where it has been suggested that the cementing action is due to secondary silica. This cemented feature of the parent material is associated with the geological origin and is in no way related to a pan formation.

TABLE 9.—ANALYSIS OF GRASSLAND SOILS OF TRANQUILLE RANGE

Soil zone	Horizon	Depth	SiO_2	Fe_2O_3	Al_2O_3	CaO	MgO	K_2O	Na_2O	P_2O_5	Organic Carbon	Organic matter O.C.=1.724	N	CO_2	pH
		in.	%	%	%	%	%	%	%	%	%	%	%	%	
Brown Earth	A_1	0–10	59.45	8.10	12.93	3.55	2.83	2.37	2.37	0.27	1.75	3.02	0.19	0.09	7.89
	†		63.01	8.58	13.71	3.76	3.00	2.51	2.51	0.29					
	B_1	10–21	50.85	8.21	12.05	9.84	4.31	1.90	2.04	0.29	0.41	0.71	0.08	5.05	8.28
	†		53.39	8.62	12.65	10.33	4.53	1.99	2.14	0.30					
	B_2	21–27	50.64	8.74	11.76	8.59	5.09	1.73	2.41	0.27	0.27	0.47	0.03	4.57	8.25
	†		51.65	8.91	11.99	8.76	5.19	1.76	2.46	0.28					
	C	27–	53.54	9.08	12.98	7.31	4.62	1.89	2.70	0.26	0.34	0.59	0.02	4.05	8.33
	†		55.15	9.35	13.36	7.59	4.76	1.95	2.75	0.27					
Dark Brown	A_1	0–8	56.93	8.55	13.20	4.00	3.57	2.09	2.56	0.31	2.10	3.62	0.25	0.06	8.18
	†		60.92	8.99	14.12	4.28	3.82	2.24	2.74	0.33					
Earth	B_1	8–14	51.94	7.84	14.96	4.29	4.50	2.24	2.71	0.35	1.83	3.16	0.23	0.22	8.52
	†		55.58	8.39	16.00	4.59	4.82	2.40	2.90	0.37					
	B_2	14–29	45.89	7.73	13.65	12.47	4.28	1.40	2.42	0.35	0.56	0.97	0.04	7.25	9.41
	†		47.27	8.03	14.61	13.34	4.41	1.44	2.49	0.36					
	C	29–	50.48	8.44	13.75	9.11	4.39	1.94	2.73	0.32	0.30	0.52	0.02	4.68	9.05
	†		51.49	8.61	14.02	9.29	4.48	1.98	2.78	0.33					
Black Earth	A_1	0–8	47.11	9.34	11.96	5.14	6.17	2.27	2.34	0.50	5.20	8.96	0.58	0.04	7.10
	†		54.65	10.83	13.87	5.96	7.16	2.63	2.71	0.58					
	B_1	8–20	50.22	11.21	12.55	5.14	8.54	1.77	2.29	0.30	1.24	2.14	0.10	0.00	7.38
	†		52.73	11.77	13.18	5.40	8.97	1.86	2.40	0.31					
	B_2	20–30	49.14	9.73	11.21	7.10	10.00	1.38	2.30	0.24	0.79	1.36	0.06	1.67	8.39
	†		51.11	10.12	11.66	7.38	10.40	1.43	2.39	0.25					
	C	30–	47.55	13.98	19.31	4.11	2.83	1.29	1.79	0.34	0.56	0.97	0.04	2.03	8.50
	†		49.45	14.54	20.08	4.17	2.94	1.34	1.86	0.35					

† Calculated to mineral constituents only.

Chemical Characteristics

The total analysis of the grassland soils is presented in Table 9. These figures give a comparison of the genetic development occurring in one parent material under three climatic zones.

It will be noted first that the depth of calcium accumulation in the profile increases from the Brown Earth to the Black Earth. In the Brown Earth the greatest accumulation takes place between 10 and 21 inches, in the Dark Brown between 14 and 29 inches, and in the Black Earth between 20 and 30 inches. Magnesium behaves similarly to calcium but to a less exaggerated degree. The figures for carbon dioxide indicate that only a fraction of the divalent bases are present as carbonates and thus the parent minerals are probably rich in basic elements.

In the Black Earth zone the presence of increased amounts of calcium and magnesium without a corresponding carbon dioxide content would suggest that they are present in insoluble form. Their presence in such abundance may be due to an uneven mixture of the original basic minerals in the profile.

Silicates, sesquioxides and sodium appear to be relatively immobile.

Organic matter is highest in the Black Earths, and within the profile it tapers off gradually with depth. The total organic matter decreases from the Black Earth to the Brown Earths, but within the profile the organic matter tapers off sharply in the Dark Brown and Brown Earths with increasing depth.

The nitrogen figures follow the same trend as organic matter. The carbon-nitrogen ratio is about 9 in all three zones. Russell (15) quoting Remezov indicates that the ratio decreases from Black to Grey Desert soils.

Potash is richest in the A horizon of all three soils as a result of the decay of vegetation. It is an illustration of the natural conservation in grassland soils.

The Black Earths are distinctly richest in total phosphates, followed by Dark Brown and Brown Earths. Data on available phosphates shown in Table 10 show that they are present in reverse order to total phosphates, Brown Earths being richest and Black Earths poorest. It is apparent, therefore, that the high phosphate content of the Black Earths is largely unavailable. Dunnewald (8) reporting on the same soils described by Thorp (20) found available phosphates to be present in a similar order. These phosphate values appear to be high compared to Prairie soils of the same genetic type.

The pH values (Table 9) are interesting in that the unfavorable physical structure of the Dark Brown Earths is associated with a high degree of alkalinity. It will be noted that these values increase from pH 8.0 at the surface to pH 9.4 in the B_2 horizon. There is no significant accumulation of sodium. Exchangeable sodium, shown in Table 10, is higher in the B_1 and B_2 horizons than in the surface, yet quantitatively it is low. This leaves the relatively high magnesium content as the only source of the alkalinity. The high alkalinity probably causes a peptization of the soil colloids which contributes to the unfavorable structure of the B horizon.

TABLE 10.—EXCHANGEABLE BASES AND AVAILABLE PHOSPHATES IN THE GRASSLAND SOILS

Soil zone	Horizon	Mg. equivalents per 100 g. soil					Available P_2O_5
		Ca	Mg.	K	Na.	Total	
							p.p.m.
Brown Earth	A_1	12.5	5.5	0.7	0.2	18.9	813
	B_1	33.5	12.9	0.5	0.4	47.3	939
	B_2	54.2	9.5	0.4	0.6	64.7	754
	C	26.4	10.4	0.3	0.6	37.7	738
Dark Brown Earth	A_1	15.3	5.0	0.6	0.2	21.1	328
	B_1	14.6	8.0	0.8	0.8	24.2	257
	B_2	25.0	10.9	0.3	0.8	37 0	160
	C	24.3	9.9	0.2	0.3	34.7	1026
Black Earth	A_1	24.6	8.4	0.8	0.1	33.9	245
	B_1	11.8	5.5	0.5	0.1	17.9	199
	B_2	24.6	4.5	0.2	0.1	29.4	245
	C	28.9	5.5	0.1	0.1	34.6	226

Although the exchangeable bases are dominated by calcium, this ion does not exceed 80% of the exchangeable capacity; magnesium, on the other hand, is present at a relatively high concentration. There seems to be considerable evidence that the basaltic rocks from which these soils have been derived are high in magnesium minerals, and that this element has played an important part in the development of the grassland profiles.

Exchangeable potassium is concentrated in the surface horizons. It does not vary with zones.

The Black Earth A_1 horizon has the highest equivalent of exchangeable bases. This can be expected from the high organic content. It is surprising to find, however, that this abundance does not continue with depth. On the basis to the solum (A and B horizons), the Brown and Dark Brown profiles have a higher total exchangeable base content than the Black Earth profile.

FOREST SOILS

Profile Descriptions

Above the upper limit of the Black Earth soil there is an abrupt change to forested podsolic soils. Three distinctive profiles are encountered with increasing elevation. Each has its characteristic vegetation. For the purpose of this paper the profile occurring immediately above the Black Earth is called the Lower Podsol. It extends from 3200 feet to 4000 feet elevation. The second type extends from 4000 to 5800 feet and is called the Middle Podsol. The third profile occurs between 5800 and 6100 feet, the upper limit of the range and is called the Upper Podsol.

The most interesting feature of these profiles is that while all are definitely podsolic, each had independent and characteristic features. They have developed from a common glacial till, hence the morphological and vegetational changes that take place with increasing elevation suggest definite climatic zones. It is believed, therefore, that the characteristic

morphological features are a reflection of the relative intensity of the dynamic podsol producing system, as it occurs in each of these three profiles.

The following is a brief description of the profiles.

Lower Podsol

Horizon	Depth	
A_0	$1\frac{1}{2}''$	Dark brown organic mat, partially decomposed and fibrous.
A_2	$0–2\frac{1}{2}''$	Ash grey loam, gritty, structureless and porous.
B_1	$2\frac{1}{2}–10''$	Light yellow brown (creamy coloured) loam, amorphous and slightly dense.
B_2	$10–25''$	Drab brown clay loam, dense, tough, large angular nut structure.
C	$25''$	Grey brown loam, unweathered, strongly cemented glacial till. The top inch may contain free lime streaks.

Middle Podsol

A_0	$1''$	Dark brown organic mat, partially decomposed and fibrous.
A_2	$0–1''$	Ash grey loam, gritty, slightly compacted and structureless.
B_1	$1–5''$	Bright orange red sandy loam, single grained and porous.
B_2	$5–15''$	Drab brown loam, dense, tough prismatic structure.
C	$15''$	Grey brown loam, unweathered, strongly cemented glacial type, containing no visible lime.

Upper Podsol

Horizon	Depth	
A_0	$3''$	Dark brown to black organic mat, partially decomposed and contains many living roots.
A_2	$0–4''$	Dark iron grey sandy loam, single grained, high in organic matter.
B_1	$4–11''$	Dark orange brown sandy loam, single grained and porous. Contains much iron-humus coated gravel.
B_2	$11–18''$	Drab brown loam, slightly dense and weakly granular in structure.
C	$18''$	Grey brown loam, unweathered, strongly cemented glacial till.

All three profiles contain basaltic, sub-angular stones and gravel.

Morphological Features

The organic horizons of the Middle and Lower Podsols are similar in that both are fibrous, incompletely decomposed mor types. L and F horizons are distinct but the H horizon is superficial, seldom attaining measurable thickness. The organic layer is sharply differentiated from the mineral soil.

In the Upper Podsol the organic layer is also a mor type. There is a sparse litter layer intimately associated with a complete cover of living herbs, mosses and lichens. The F layer is deep, and while it is incompletely decomposed, it differs from the previous two types in that it is composed of finer, less woody fibre and is matted with living fine surface roots. Decomposition increases with depth but the transition to an H layer is indistinct. The organic matter penetrates into the mineral soil to a considerable depth. In the mineral soil the organic matter is finely

FIGURE 8. Fairly open stand of mature Douglas fir in Montane zone. Note abundance and good growth of herbaceous vegetation.

FIGURE 9. Alternate forested and open areas in Upper Subalpine zone at an altitude of 6000 feet. The principal tree is Engelmann spruce, while the openings are dominated by grasses and sedges.

divided, much of it being colloidal especially below the A_2 horizon. Unlike a mull type of humus, no crumb structure is formed, the soil particles remaining single grained.

There is a well developed ash grey leached layer in both the Lower and Middle Podsols. In the former, the A_2 horizon is loose and dusty, while in the latter profile the leached layer is slightly compacted, whiter, and has the clean appearance of washed sand.

The A_2 horizon of the Upper Podsol resembles an A_1 in that it is dark coloured and high in organic matter. The chemical analysis, however, shows this layer to be leached of sesquioxides. It is probable that the ash grey colour has been masked by an organic coating.

The three podsol sub-types were largely identified and mapped by the conspicuous colours of the B_1 horizons. These colours changed from a lustreless yellow and grey brown to a bright orange red and finally to a dark orange brown, with increasing elevation. The change of colour from one zone to another was sharp and easily identified.

The structure was single grained in each case, except in the Lower Podsol zone where a weak fine crumb occurred.

The B_2 horizons of all three zones were characterized by an accumulation of clay, and the presence of a well defined structure. There appeared to be no consistency in the relative amounts of accumulated clay between the different zonal profiles. The strongest structural development occurred in the Middle Podsol zone.

The occurrence of free lime as streaks over the impervious C horizon was a fairly consistent feature of the Lower Podsol. Free lime accumulation did not occur in the other podsol zones.

The Upper Podsol profile belongs to a sub-order that has been described as wet podsol, humus podsol, and mountain meadow soil. Joffe (11) described mountain meadow soils as a type of formation unique inasmuch as it has no equivalent in the horizontal zonal distribution of soils.

Three vegetation types are associated with the Upper Podsol zone. No profile differences were noted except that in the treeless meadow phase the A_0 and A_2 horizons were merged into a mineral horizon, very high in organic matter, but shallower than the combined A_0 and A_2 horizons of the forested phase.

In all three phases of the Upper Podsol, drainage was unimpaired except for the impervious C horizon, and there was no indication of a glei horizon. Numerous semi-bogs occur in the area with conspicuous glei horizons, but these form a distinct association not dealt with in this paper.

Chemical Characteristics

The fundamental difference between the Lower and Middle Podsols would seem to be associated with the nature of the organic matter, for most of the characteristic features can be explained on this basis. In the Lower Podsol zone there is a mixture of hardwood and softwood litter,

TABLE 11.—ANALYSIS OF PODSOL SOILS OF TRANQUILLE RANGE

Soil zone	Horizon	Depth in.	SiO_2 %	Fe_2O_3 %	Al_2O_3 %	CaO %	MgO %	K_2O %	Na_2O %	P_2O_5 %	Organic carbon %	Organic matter O.C. $\times$ 1.724 %	N %	CO_2 %	pH
Lower Podsol	A_0	2	48.21	5.17	8.35	2.58	3.10	0.94	1.18	0.15	11.97	20.64	0.46	Nil	5.82
	†		65.38	7.00	11.30	3.49	4.20	1.27	1.60	0.20					
	A_2	0–2½	63.67	5.98	13.28	2.66	2.83	1.93	1.97	0.16	1.63	2.81	0.09	Nil	6.48
	†		67.00	6.30	14.00	2.80	2.98	2.03	2.07	0.17					
	B_1	2½–8	60.06	7.56	14.97	2.95	2.24	1.50	2.04	0.21	0.99	1.71	0.08	Nil	6.24
	†		62.80	7.91	15.65	3.08	2.34	1.57	2.14	0.22					
	B_2	8–23	52.88	12.16	16.01	3.58	4.15	1.74	1.47	0.25	0.51	0.88	0.04	Nil	7.15
	†		54.90	12.60	16.60	3.72	4.30	1.80	1.52	0.26					
	C	23–	54.04	11.30	15.94	4.40	5.34	1.94	2.21	0.29	0.24	0.42	0.03	Nil	6.95
	†		55.70	11.65	16.42	4.54	5.50	2.00	2.27	0.30					
Middle Podsol	A_2	0–1	67.41	4.13	13.17	2.53	1.29	2.39	3.15	0.13	2.71	3.97	0.13	Nil	5.49
	†		72.60	4.45	14.20	2.73	1.39	2.58	3.40	0.14					
	B_1	1–5	51.08	9.08	18.54	2.68	1.45	1.92	2.63	0.84	3.82	6.69	0.17	0.02	5.88
	†		57.60	10.22	20.90	3.02	1.64	2.17	2.98	0.95					
	B_2	5–15	49.66	14.94	16.18	3.80	3.15	2.12	3.43	0.24	0.63	1.09	0.04	Nil	6.62
	†		51.50	15.50	16.79	3.94	3.26	2.20	3.56	0.25					
	C	15–	50.36	13.74	18.94	5.07	2.74	1.87	3.28	0.30	0.18	0.31	0.04	Nil	7.42
	†		51.51	14.10	19.40	5.20	2.80	1.92	3.36	0.31					
Upper Podsol	A_2	0–7	42.60	9.53	14.19	2.98	1.92	1.39	2.50	0.34	12.16	20.96	0.52	Nil	4.87
	†		54.60	12.20	18.20	3.82	2.46	1.78	3.20	0.44					
	B_1	7–14	46.32	13.69	18.54	4.26	2.70	1.64	2.89	0.32	2.78	4.79	0.17	Nil	5.60
	†		50.60	14.90	20.30	4.66	2.95	1.79	3.16	0.35					
	B_2	14–21	46.68	13.79	19.96	4.40	2.69	1.60	3.25	0.39	0.88	1.52	0.06	Nil	6.05
	†		48.80	14.40	20.82	4.60	2.86	1.67	3.39	0.41					
	C	21–	52.49	13.18	18.09	4.55	4.65	1.77	3.08	0.43	0.25	0.43	0.03	0.05	7.05
	†		53.90	13.50	18.60	4.68	4.79	1.82	3.16	0.44					

† Calculated to mineral constituents only.

plus the annual accumulation from a luxurious herbaceous cover. The decomposition of such material will produce a humus of relatively high base status. The organic layer of the Middle Podsol profile has been derived from a coniferous forest, in which hardwoods are absent. The understory of shrubs and herbs is sparse.

It is to be expected, therefore, that the decomposition products will form a raw acid humus. This supposition is borne out in several respects by the chemical analysis shown in Table 11. The degree of acidity is shown to be appreciably greater in the Middle Podsol profile. Further, it will be noted that the organic matter in the Lower Podsol zone has not been eluviated to the same extent as in the Middle Podsol zone. In the former case organic matter decreases quickly with depth, indicating a stable colloidal form, while in the latter case organic matter accumulates in the B_1 horizon from a dispersed state.

Dispersed humus colloids through their protective action influence the leaching of iron oxide. Reference to Table 11 shows the leaching of sesquioxides to have taken place in all three profiles, and in respect to the two first profiles, it is quite apparent that eluviation is greatest in the Middle Podsol zone. The relative amount of sesquioxide to silica is shown in Table. 12. It will be seen that the B_2 is the horizon of greatest accumula-

TABLE 12.—SILICA SESQUIOXIDE MOLECULAR RATIO IN MINERAL CONSTITUENTS OF FOREST SOILS

Soil zone	Horizon	SiO_2/R_2O_3	SiO_2/Fe_2O_3	SiO_2/Al_2O_3
Lower Podsol	A_0	7.0	24.6	9.8
	A_2	6.3	28.4	8.1
	B_1	5.1	21.0	6.8
	B_2	3.8	11.5	5.6
	C	4.0	12.7	5.7
Middle Podsol	A_2	7.2	43.0	8.6
	B_1	3.5	14.9	4.7
	B_2	3.3	8.8	5.2
	C	3.1	9.7	4.5
Upper Podsol	A_2	3.5	11.7	5.1
	B_1	2.9	8.9	4.2
	B_2	2.8	9.0	4.0
	C	3.3	10.5	4.9

tion. A comparison of the Lower and Middle Podsols shows the latter soil type to have suffered the greatest losses of iron and aluminium from the A_2 horizon.

The analysis of exchangeable bases is shown in Table 13. It will be noted that the Lower Podsol contains a greater number of base equivalents

Table 13.—Exchangeable bases and available phosphates in forest soils

Soil zone	Horizon	Mg. equivalent per 100 g. soil				Available P_2O_5
		Ca	Mg	K	Total	
						p.p.m.
Lower Podsol	A_0	15.3	8.4	0.7	24.4	174
	A_2	5.7	3.5	0.5	9.7	80
	B_1	5.7	3.5	0.5	9.7	110
	B_2	12.5	10.9	0.3	23.7	429
	C	11.1	10.9	0.2	22.2	697
					65.3	
Middle Podsol	A_2	3.6	1.0	0.2	4.8	72
	B_1	5.7	2.0	0.3	8.0	192
	B_2	10.0	5.0	0.2	15.2	292
	C	12.5	6.5	0.2	19.2	875
					47.2	
Upper Podsol	A_2	2.4	1.0	0.2	3.6	24
	B_1	1.8	0.5	0.1	2.4	29
	B_2	7.1	2.0	0.1	9.2	229
	C	11.4	5.0	0.1	16.5	1203
					31.7	

than the Middle Podsol profile, indicating the importance of the base status of the humus layer as a source of supply. These figures illustrate the degree of leaching in two ways, first by the depletion of bases from the A_2 horizon and second, by the depth of the accumulation zone. The A_2 of the Lower Podsol appears to be less leached than the Middle Podsol and the horizon of accumulation is the B_2. In the Middle Podsol, accumulation occurs in the C horizon. The intensity of leaching is greatest, therefore, in the Middle Podsol zone.

Unfortunately Table 13 does not show the base exchange capacity, hence it is impossible to compare the degree of saturation of the two soils. For the same reason no comments can be made on the organic versus inorganic colloids, or on the destruction of the absorbing complex through the leaching of sesquioxides.

The analytical data show that the influence of the humus base status on soil reaction, degree of dispersion, and intensity of leaching is most important. This feature should be of prime significance in determining podsol sub-zones.

The Upper Podsol appears to be differentiated from the others on the basis of a lack of weathering rather than intensity of leaching.

The climatic conditions are somewhat tundra-like in that the soil is snow covered and frost bound for nearly nine months of the year, and

summer frosts are frequent. Such conditions are not conducive to physical, chemical or biological action. This is well brought out by the analytical data.

In the first place the high organic content of the A_0 and A_2 horizons suggests that biological decomposition cannot keep pace with the annual accumulation. The A_0 horizon is a 3-inch organic mat, while from Table 11 it will be seen that the A_2 horizon contains nearly 21% organic matter. That this is a raw acid humus is shown by the pH values (Table 11). It will also be noted that the movement of organic matter persists to great depths.

In respect to the eluviation of sesquioxides it will be noted from Table 11 that accumulation has taken place in both B_1 and B_2 horizons, whereas in the other podsol types accumulation occurred mainly in the B_2 horizon. The suggestion that a lack of physical and chemical weathering is a feature of this zone is amplified by the figures for sesquioxide movement. The amount is small compared to the Middle Podsol profile. This is in spite of a low pH value and a raw acid humus layer, the conditions favouring intensive leaching. The figures in Table 12 show that while sufficient leaching has taken place to indicate podsolization, the differentiation between the A and C horizons is slight.

From Table 13 it will be seen that exchangeable bases are very low and tend to accumulate in the C horizon. The high organic content of A_2 must be extremely unsaturated for such low values to be attained. The depth to which organic matter is carried and the accumulation of exchangeable bases in the C horizon suggest the intensity of leaching to be greatest in the Upper Podsol zone. However, from the slight movement of sesquioxides it must be concluded that podsolization in this zone is restricted by the short season during which active weathering may take place.

Pearson (9) found that forest soils in Arizona tended to be deepest in the lower zones, weathering being hampered by low temperatures at higher altitudes. Soils in all zones above the ponderosa pine association tended to be thin and relatively coarse in Arizona. On the Tranquille range, the soils of the Montane zone are as deep and well developed as those of the zones below, and only in the Upper Subalpine is there any marked decrease in profile development.

The pH values found by Pearson under conditions of vertical zonation in Arizona were 8.2 in the top 6 inches of grassland soil, 7.0 in the Douglas fir (Montane) zone, and 6.5 in the Engelmann spruce (Subalpine) zone. These values correspond fairly closely to those determined for the soils of the Tranquille area (Tables 9 and 11).

SOIL-PLANT ZONAL BOUNDARIES

The boundaries between both soil and plant zones were fairly distinct and no wide transition belts occurred. These boundaries follow the contour of the land remarkably closely where the exposure is uniform.

Grassland Zones

The limitations of grassland soil zone distribution due to exposure are interesting. Brown Earths are to be found chiefly on south and west

exposures. Gently sloping north and east exposures in the Brown Earth zone are characterized by an invasion of Dark Brown Earths. On the south side of the Kamloops valley, Brown Earths having a northerly exposure occur. Their upper limit, however, is about 300 feet below the average level on south and west slopes.

A similar invasion of Black Earths into the Dark Brown Earth zone occurs on gentle north and east slopes.

The best development of the Black Earth profile is to be found on gently sloping and level ground. Crests and ridges are frequently very dark brown rather than black in colour. Where north and east exposures occur on steep slopes there is an abrupt change to forested podsol soils.

It has already been noted that the succession of soil zones on mountainous grasslands is more or less similar to that of level topography. The boundaries are governed by elevation rather than latitude. In this respect Thorp (20) provides an interesting comparison for a similar succession in Wyoming.

	Big Horn, Wyoming	Tranquille, British Columbia
Brown Earth	5000–5500 feet	1100–2300 feet
Dark Brown Earth	5500–6500 feet	2300–2800 feet
Black Earth	6500–7700 feet	2800–3200 feet

The Big Horn Range is at Latitude 44 while the Tranquille Range is at 51, a difference of 7 degrees of latitude.

Plant zonation in the grasslands shows the effect of slope and exposure in much the same manner as do the soils. The vegetation of each association tends to intrude into that of the zone above on warm, dry slopes and to extend into the zone below on cool, moist exposures. Depressions in the Middle Grassland zone are occupied usually by Upper Grassland species including Kentucky bluegrass and graceful sedge and have a Black Earth profile. Forest vegetation extends well into the Upper Grassland zone on North and east slopes.

Pine Savanna

A marked variation of the normal zonal succession occurs on the east side of the Tranquille River (Figure 1) at an altitude of 2100 to 3000 feet. Here a ponderosa pine savanna occurs immediately above the Lower Grassland association and below the Montane zone. The Middle and Upper Grassland types are not present in this area. The soil in the pine savanna closely resembles the Dark Brown Earth usually associated with Middle Grassland vegetation. Black Earths do not occur.

The vegetation of this type consists of ponderosa pine forest with a well developed ground cover dominated by perennial bunchgrasses, mainly bluebunch wheatgrass, rough fescue and Junegrass. The tree stand is extremely open at the lower edge of the zone and its density increases gradually with altitude to the point where it merges with the Montane forest. A similar vegetation and soil complex has been noted in several portions of Southern British Columbia, including the Thompson, Nicola and Okanagan valleys. This association appears to represent the northern

fringe of the ponderosa pine zone which occupies extensive areas farther south in the Rocky Mountain region.

No detailed study was made of the factors responsible for the occurrence of this type. No marked difference in soil conditions was apparent, although on the average soil texture was a little coarser, stones more plentiful and pH a little lower than for comparable grassland soils. The pine savanna is most common on fairly coarse soils, often at the foot of steep slopes where seepage from above tends to increase sub-soil moisture. Apparently the type is associated with a climatic tension zone between forest and grassland, and its presence or absence seems to be determined by relatively small local differences in climate and soils.

Forest Zones

Only a brief study was made of the influence of exposure upon the distribution of soils in the forested region, as the area is relatively inaccessible and served by only two pack trails. One feature noted was that the best development of the Upper Podsol occurs on the rolling plateau at the highest elevation. This may be an influence of exposure and topography, but on the other hand it is possible that the maximum development occurs only at 6000 feet and over.

As in the grassland area, local conditions of slope and exposure affect zonal boundaries. The Montane forest ascends 300 or more feet above its normal altitudinal limits on south and west slopes. Conversely, the Subalpine zone descends considerably along narrow stream valleys where the topography tends to produce moister and cooler conditions.

The most striking feature of zonation in the Upper Subalpine is the occurrence of treeless openings, often called "mountain parks" (6). As noted earlier, some of these are potential forest sites, recovering slowly from destruction by fire. There still remain many openings occupied by grasses and grass-like plants where there is no evidence of past occupation by forest or present trend in that direction. The vegetation is low growing, and is characterized by a number of alpine species, including mountain hairgrass, alpine timothy and sibbaldia. The soils of the openings appear to be essentially similar to those of the forested portions of the zone.

Similar mountain parks in the Subalpine zone have been described by investigators in the Rocky Mountain region, and various theories have been advanced to account for their occurrence. Poor soil aeration and a microclimate unsuitable for tree growth are common explanations. Although drainage is good in the openings in the Tranquille Subalpine zone, the sharpness of the line between forest and treeless areas suggests that edaphic factors may be involved. In addition, the microclimate of the openings may differ enough from that of the remainder of the zone to affect plant life critically. Dixon (7) who found a similar vegetation at high altitudes in Utah, points out that these openings, being located in basins and shallow valleys, tend to be cooler and moister than adjacent areas.

Zonation in Other Areas

Brief studies of grassland areas in other parts of southern British Columbia indicated that the zonal sequence found on the Tranquille range

is of general occurrence. In the Kamloops district and in the Nicola and Okanagan Valleys to the south and southeast of Kamloops, marked agreement was found in the nature of both soils and vegetation. The altitudinal limits of the zones varied with local topographic and climatic conditions.

Less opportunity was afforded for soil-plant studies of forest vegetation in other areas. Limited observations indicated that, as in the case of the grasslands, the zonal types found on the Tranquille Range are of general occurrence in southern British Columbia.

SOIL-PLANT RELATIONSHIPS

Climatic Influences

The marked changes in climate occurring at different altitudes on the Tranquille Range were discussed in the introduction of this paper. It was noted that moisture conditions are the principal factors limiting growth at lower altitudes, including all the grassland zones.

Data concerning the relationship of the atmospheric moisture conditions to soil composition and plant production are presented in Table 14.

TABLE 14.—P/E RATIO IN RELATION TO PLANT YIELD AND SOIL NITROGEN

Soil plant zone	P/E ratio	Forage yield per acre	Soil nitrogen of A horizon
		lb.	%
Brown Earth Lower Grassland	6.4	375	0.19
Dark Brown Earth Middle Grassland	10.0	560	0.25
Black Earth Upper Grassland	20.0	1200	0.58

The P/E ratio is generally considered to be one of the best indices of the external moisture conditions affecting plant life (12). It is apparent that on the Tranquille grasslands both plant production and soil fertility are affected greatly by moisture conditions. From Table 14 it is evident that with an increasing precipitation efficiency there is a denser vegetation and under natural conditions, a more fertile soil.

Some data were obtained on soil moisture reserves at the beginning of the growth periods of 1939 and 1940. A comparison of these figures with the depth of the layer of lime accumulation is shown in Table 15.

TABLE 15.—AVAILABLE SOIL MOISTURE AND DEPTH OF LIME ACCUMULATION

Soil plant zone	Available soil moisture				Depth of lime layer
	0–6 ins.	6–12 ins.	12–18 ins.	18–24 ins.	
	%	%	%	%	in.
Brown Earth Lower Grassland	7.3	6.0	1.9	0.5	10
Dark Brown Earth Middle Grassland	17.5	8.1	3.7	2.1	14
Black Earth Upper Grassland	24.6	10.8	10.0	9.8	20

The depth of the lime accumulation is evidently a good indication of the lowest depths of appreciable soil moisture, in so far as plant roots are concerned. This is brought out in Table 9 also where the depth of organic matter, largely decayed roots, is shown to coincide with the depth of useful amounts of soil moisture.

FIGURE 10. *(a)* Soil profile in Middle Grassland zone, Tranquille Range. *(b)* Soil profile in Middle Podsol zone, Tranquille Range.

In the Montane zone, as in the grasslands, moisture conditions are of prime importance. The growing season is still sufficiently long for the full seasonal development of a varied flora, while soil moisture is often deficient particularly in the late summer. In the Subalpine and Upper Subalpine types, however, temperature seems to be the dominant factor. Soil moisture is usually abundant, but shortness of growing season and low air and soil temperatures restrict plant and soil development. According to

Thornthwaite's (19) system of climatic classification, the Subalpine zone is in the "Taiga" class in which low temperature efficiency is the major limiting factor. The Montane zone is classified in the "Microthermal" group, coolest of those climates in which precipitation effectiveness is still the prime factor.

The climatic conditions prevailing in the Montane zone are reflected in the presence of a fairly open cover of coniferous and deciduous trees, along with the development of a rich shrub and herb flora. This vegetation in turn influences soil development, through the medium of a relatively high lime humus, with production of the characteristic Lower Podsol profile.

In the Subalpine, climate favours the production of a fairly dense stand of coniferous trees with a sparse understory of shrubs and herbs and a well developed ground cover of mosses and lichens. This in turn results in the formation of a raw, acid humus and a soil profile in which leaching is more pronounced than in the Lower Podsol.

In the Upper Subalpine, temperatures are still more extreme, while evaporation is probably greater than in the Subalpine. Conditions are less unfavourable for tree growth, with the result that the vegetation consists of patches of relatively dwarfed coniferous forest interspersed with treeless openings. The soil profile formed under these conditions is characterized by a high content of organic matter in the surface horizons and by a lack of weathering.

Soil-Plant Relationships within the Zones

Within the grassland zones, the soil characteristics of most importance in respect to the plant cover were those associated with the moisture factor. Depth of the solum appeared to be of outstanding importance in this regard. The vegetation of shallow soils was characterized by the presence of xeric species and by sparse cover and poor growth.

Slight differences in soil texture had no apparent effect on the plant cover, but marked differences affected both species composition and productivity. Very fine soils were rare on the study area, but sandy and gravelly types were fairly common. Species associated with these coarse soils included sand dropseed, three-awned grass (*Aristida longiseta*), Indian ricegrass (*Oryzopsis hymenoides*), sumach (*Rhus glabra*), balsam root and *Erigeron compositus*.

A number of the dominant species were good indicators of soil conditions. Sagebrush, for instance, occurred widely in the Lower Grasslands, but formed tall, dense stands only on soils of good depth and moisture content. Kentucky bluegrass and Columbia speargrass, although co-dominant over much of the Upper Grassland zone, differed considerably in habitat requirements. The bluegrass dominated on low-lying areas of deep soil and good moisture conditions, while the speargrass was most abundant on drier sites with relatively shallow, coarse soils. Bluebunch wheatgrass was dominant on practically every type of soil in each of the three zones. However, there were marked differences in density, height and yield depending on soil depth and texture. Clipped plots of this species in the Lower Grassland zone yielded 67% more forage on a site with a fairly deep loam soil than on an area with a shallow, sandy loam profile.

Soil reaction did not appear to be strongly significant. In the Lower and Middle Grasslands some surface soil ratings were as high as pH 8.4 with pH 9.4 in the C horizon. These alkaline conditions had no marked effects on the distribution of plant species but appeared to cause some reduction in plant cover and production.

In the forest, variations in soil conditions within the zone were not marked in the relatively limited area covered by the study. Shallow, gravelly soils were indicated by open stands and poor growth of trees and by the abundance of such ground cover species as kinnikinnick. In general, aspen was most abundant on soils of relatively good depth and fine texture.

Range Utilization in Relation to Vertical Zonation

It has been pointed out that there is a succession of climatic changes from the lowest to the highest elevations on the Tranquille Range and in southern British Columbia generally. As a result of these climatic differences there is a vertical zonation of vegetation and soils.

In the utilization of range lands, vertical zonation must be taken into account in any program which aims at securing maximum use of grazing resources without depletion. The characteristics of the various zones in relation to grazing use are discussed briefly in the following section.

In the Lower Grassland zone, bluebunch wheatgrass is the principal species. On the Tranquille Range (21) the average date of first growth is mid-March. The readiness for grazing stage (plants averaging 6 inches in height) is reached a month later. Active growth is usually finished by the end of June, and curing follows in July or August. Fresh fall growth supplements the dry forage in most years. This is the least productive of the grassland zones.

The Middle Grassland zone is similar in many ways to the Lower Grassland type. Bluebunch wheatgrass and common speargrass are the principal forage species. Growth begins about 10 days later than in the lower zone and curing is correspondingly delayed. The grazing capacity is greater than at lower elevations, but only about one-half that of the Upper Grassland zone.

The Upper Grassland type contains a variety of forage species of which bluebunch wheatgrass, rough fescue, Columbia speargrass and Kentucky bluegrass are the principal forms. Growth begins nearly two weeks later than in the Middle Grasslands and the date of readiness for grazing is correspondingly later, averaging about mid-May. Much of the forage usually remains green during the entire summer. This is the most productive of the grassland zones, with a grazing capacity three times as great as that of the Lower Grassland type.

The Montane forest zone provides a considerable amount of grazing due to the presence of a well developed understory of shrubs and herbs. Pine grass constitutes half or more of the available forage, but many broad-leaved plants including rose, spiraea, rough aster, hawkweed, lupin, peavine and vetch are eaten. Growth begins later than in the grassland zones, and the readiness for grazing stage is not reached until mid-June. The yield of forage is approximately the same as for the Lower Grassland and

the grazing capacity is probably similar, although not much is known at present of the long-term productivity of timber ranges.

The Subalpine zone is in general unsuited for grazing as the herb and shrub cover is relatively sparse and contains a high proportion of unpalatable species. The Upper Subalpine type is better adapted to grazing, due to a greater abundance of forage and to the presence of treeless openings. Since the growing season is short, the period of use is confined mainly to July and August. Sheep are often grazed in both the Upper Subalpine and Alpine zones.

It is evident that the natural grazing sequence for a range containing vertical zones should be based upon the occurrence of successively shorter seasons of growth and cooler climate at higher altitudes. The marked differences in grazing capacity of the various zones need to be considered also.

A suitable grazing plan for a range such as the Tranquille would involve using the Lower Grassland zones from mid-April to early May and the Middle Grasslands until the end of May. The Upper Grasslands would be utilized during June and the Montane Forest from late June until the end of September. In October the Upper Grassland zone would be grazed again, followed by the Middle and Lower Grasslands in November and on into the winter if sufficient forage were available. A grazing program similar to this was carried out on the Tranquille Range (21) for several years with marked benefits to both vegetation and livestock.

Where proper range use is not practised, depletion of vegetation and soils is bound to occur. On the Tranquille grasslands, marked changes in plant cover and considerable soil erosion have occurred as a result of improper grazing for a period of nearly 60 years. Overgrazing has resulted in a great decrease in the abundance and vigour of the perennial grasses and a corresponding increase in unpalatable species. The details of the provess vary with each zone.

The most striking change produced by overgrazing in the Lower Grasslands has been the decrease in abundance and vigour of bluebunch wheatgrass and the increase in sagebrush. Dwarf everlasting, pasture sage and cactus have increased also.

Most of the perennial grasses of the Middle Grassland zone have decreased greatly with overgrazing, but dwarf bluegrass (*Poa secunda*), due to its short stature and low palatability, has not been affected as much as more desirable species. Weed species which have increased greatly include downy bromegrass, rabbit brush, pasture sage and dwarf everlasting.

The vegetation of the Upper Grasslands is less readily affected by overgrazing than is that of the two lower zones and the changes have been less drastic. Two of the dominants, bluebunch wheatgrass and rough fescue have declined greatly with overgrazing, but the other two, Columbia speargrass and Kentucky bluegrass have persisted to a surprising degree. Unpalatable forms which have increased include species of everlasting, fleabane and dandelion.

Grazing of the forest zones of the Tranquille Range has not been sufficiently heavy to produce significant changes in plant cover. On this range, as in many others in southern British Columbia, the grazing resources

of the forest zones were not utilized to any extent until quite recently. At the same time it is apparent that misuse of the timber ranges would result in deterioration of the forage cover.

In relation to soil conservation, overgrazing is a serious cause of erosion, ample evidence of which was found on the Tranquille grasslands. On both grassland and forest ranges, destruction of the plant cover leads not only to erosion but also to drought through accelerated run-off and a general lowering of the water table. When the balance between soil, vegetation and climate is upset by the misuse of land, a vicious cycle commences that ends with the destruction of the soils ability to maintain vegetation. The Lower and Middle Grassland zones in particular, due to the dry, warm climate under which they exist, are highly susceptible to the ill effects of overgrazing.

SUMMARY

The observations obtained from a soil plant survey of the Tranquille Range in the southern interior of British Columbia are presented, together with analytical data in support of the findings.

The study was confined chiefly to an area having a general southerly exposure and a range in elevation from 1100 feet to 6100 feet.

It was found that temperature and the frost-free period decrease while precipitation and the P/E ratio increase with increasing elevation.

Associated with these climatic changes was found a succession of soil and plant zones.

The agreement between the respective soil and plant zones was sufficiently close to establish a definite relationship. These zones are as follows:

Altitude	Soil Zone	Plant Zone
1100–2300 feet	Brown Earth	Lower Grassland
2300–2800 feet	Dark Brown Earth	Middle Grassland
2800–3200 feet	Black Earth	Upper Grassland
3200–4000 feet	Lower Podsol	Montane Forest
4000–5800 feet	Middle Podsol	Subalpine Forest
5800–6100 feet	Upper Podsol	Upper Subalpine

The genetic development of the soil and the corresponding plant cover show that moisture is the most important climatic influence at lower elevations. There is a close agreement between plant growth and the precipitation-evaporation ratio.

With increasing elevation, temperature and the length of the frost-free period are the decisive factors determining zonal development.

The influence of elevation and exposure on the distribution of vegetational and soil zones is described.

The grassland zones are dominated by perennial bunchgrasses, particularly bluebunch wheatgrass (*Agropyron spicatum*) and belong to the Palouse Prairie Formation. The Lower Grassland type is characterized by a sparse cover, low productivity and the abundance of xeric forms such as sagebrush (*Artemisia tridentata*) and sand dropseed (*Sporobolus cryptandrus*). The Upper Grassland zone is distinguished by a richer flora,

denser cover, greater productivity and the common occurrence of relatively mesic plants such as Kentucky bluegrass (*Poa pratensis*) and graceful sedge (*Carex praegracilis*). The Middle Grassland zone is intermediate in nature between the other two types.

The forest zones are dominated by evergreen conifers. The Montane forest is characterized by stands of Douglas fir (*Pseudotsuga taxifolia*), by well-developed shrub and herb layers and by sparseness of the moss and lichen cover. The Subalpine type is distinguished by denser stands in which Engelmann spruce (*Picea Engelmanni*) and subalpine fir (*Abies lasiocarpa*) are the climax dominants. The shrub and herb strata are sparse but the moss layer is well developed.

The Upper Subalpine zone is occupied by alternating areas of forest and treeless openings. Engelmann spruce is the principal tree, while oatgrass (*Danthonia intermedia*) dominates in the openings.

The important morphological features of the grassland soils are, a shallow solum probably due to erosion and surface creep, a dense, tough solonetz-like B horizon, a high concentration of free lime close to the surface and an impervious glacial till subsoil.

The chemical data indicate that besides calcium, magnesium is present in unusually large amounts. It is suggested that the solonetz-like B horizon may be due to magnesium rather than sodium.

The podsol soil sub-zones are distinguished by the characteristic colours of the B_1 horizon. These are yellow brown, bright orange red and orange brown.

It is suggested that the genetic difference between the Lower and Middle Podsols depends largely upon the base status of the humus layer, while the Upper Podsol is differentiated by a short annual period of active weathering rather than a less intensive leaching.

The relation of vertical zonation to range utilization is discussed briefly and the changes resulting from overgrazing in the grassland zones are described.

CONCLUSIONS

The project has shown that within a limited geographical unit, a close agreement exists between soil and plant zones. To a limited extent it was shown that the texture, depth and reaction of soils within a zone may be identified by the composition and abundance of the plant cover. Similarly, much can be deduced from soil studies regarding the potential plant cover of areas on which the vegetation has been temporarily altered by factors such as grazing or fire. As a consequence the writers are of the opinion that minute as well as broad relationships may be found between the soil and the plant cover it supports.

The data indicate that both plant communities and certain characteristic species are good indicators of the habitat. The dominants of an association do not by their presence alone serve as precise indicators, since they usually extend throughout a broad type or, as in the case of *Agropyron spicatum*, may dominate in more than one zone. Density, yield and vigour are of prime importance in assessing the indicator value of dominant species.

The writers are enunciating no new theory in expressing the belief that soil and plant studies are complementary and, with experience, may be used to mutual advantage in gaining a fuller understanding of both these natural resources. These conclusions are in agreement with those of Shantz (11), Cajandar (3) and others who have found close relationships between soil and vegetation and have put these findings to practical use in land utilization, forestry, etc.

Joint soil-plant surveys seem especially suitable for broad reconnaissance work where lack of detail in the mapping of soils and vegetation may be offset by better understanding of relationships between the various types.

For range surveys, soil-plant studies are a means of describing zones, their capabilities and limitations for man's use in a most effective and practical manner. Where vertical zonation of vegetation and soils occurs, proper grazing utilization can be secured only by management practices based on the nature and relationship of the different zones. Neglect of this principle results in depletion of both vegetation and soil.

ACKNOWLEDGMENTS

The writers wish to acknowledge their appreciation and thanks to Mr. L. E. Wright, Science Service, Department of Agriculture, Ottawa, for the chemical analyses used in this paper. They are indebted to Dr. A. Leahey, Assistant (Soils), Central Experimental Farm, Ottawa; Dr. D. G. Laird, Professor of Agronomy, University of British Columbia Vancouver, B.C.; Mr. C. C. Kelley, Officer-in-Charge, British Columbia Soil Survey Branch, Kelowna, B.C., and Dr. S. E. Clarke, Agrostologist, Dominion Experimental Station, Swift Current, Sask., for assistance in this study and in the preparation of the manuscript. Assistance given in the identification of plants is acknowledged in the section on Methods of Study.

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PLANT TISSUE TESTING[1]

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[Received for publication February 10, 1944]

The chemical examination of plants as a means of determining the availability of soil nutrients and thus, indirectly, the fertilizer requirements of a crop, has long been advocated by certain workers. In 1928, Salter and Ames (2), after a study of the Neubauer seedling method, the analysis of juice from plant tissues, and Hoffer's tissue test for nitrogen and potassium, reached the conclusion that this method of approach to the problem was not of very much practical use. However, since that time, a large amount of work has been done on the use of plant analysis or tissue tests by a number of workers. Various modifications of the general methods of examining the plant itself are available, such as the foliar diagnosis procedure of Thomas (5), the spectrographic analysis method of Lundegårdh (1), the examination of plant sap, etc. Such methods involve quantitative laboratory analyses and require considerable time. A promising, relatively rapid, semi-quantitative method has been developed by Thornton *et al.* (6), and applied with apparently good results by Scarseth (3, 4).

While the longer laboratory methods are necessary in certain types of research, the more rapid semi-quantitative test which distinguishes between abundant and deficient amounts of nutrients, if found to be workable, would be satisfactory in diagnosing the fertilizer needs of a crop. In the method of Thornton, the amounts of unassimilated nitrate, inorganic phosphate and potassium in the plant tissue are measured. The tests are carried out in the following way: (a) For nitrates, a solution of diphenylamine in concentrated H_2SO_4 is applied to the plant tissue. A dark blue colour develops when nitrates are present. (b) For phosphates, the plant tissue is cut into small pieces and extracted with a solution of ammonium molybdate in HCl. When stannous chloride is added, a blue colour develops if phosphate is present. (c) For potassium, the plant tissue is cut into small pieces and extracted with a solution containing sodium cobaltinitrite, sodium nitrite and acetic acid. When ethyl alcohol is added and the solution let stand, a yellow precipitate separates out due to the presence of potassium. The interpretation of the tests is made on the basis of very high, high, medium, low and very low values, depending on the depth of colour developed by the tests.

A preliminary investigation of the application of the Thornton method was conducted on the fertilizer plots of the Division of Chemistry, Central Experimental Farm, Ottawa, during 1943. Here it was possible to compare the results of the tissue tests with the effect of fertilizer treatments on yields. An area consisting of 4 ranges was available, each range containing 2 blocks of 5 plots each. The soil was a light sandy loam, classified as Uplands sand, and had been cropped with vegetables for a number of

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years. Five treatments were used, viz., check, PK, NP, NK and NPK, which, on the 4 ranges of 2 blocks each, gave 8 replicates of each treatment. The individual plots were 1/200 acre in size. The fertilizers used and the amounts applied per plot were as follows: nitrogen as sulphate of ammonia, 1 lb.; phosphorus as 20% superphosphate, 2 lb.; potassium as muriate of potash, 1 lb. These quantities together corresponded to a mixed fertilizer of 4-8-10 composition at the rate of 1000 lb. per acre. Three kinds of plants were grown, potatoes (3 rows), tomatoes (1 row of 4 plants), and corn (2 rows).

The first part of the growing season was characterized by heavy and frequent rainfall. The appearance of the plants indicated a possible lack of nitrogen which might have been due to leaching. It was therefore decided to repeat the application of sulphate of ammonia on those plots which had received it previously.

From early in the summer, the crops showed definite response to the nitrogenous fertilizer but not to those supplying phosphoric acid and potash. The plants on all plots which received treatments of nitrogen showed much more vigorous growth than those on the other (check and PK) plots. One row of corn on each plot was used for plant tissue tests, the other being kept for yield. One row of potatoes was used for testing and the yield was measured on the other two. With the tomato plants, only one leaf from each plant was used in the testing so that all could be used for obtaining yield data.

The figures showing the yields, expressed on the basis of pounds per acre, are presented in Table 1. They show very clearly that there was little if any effect from the PK treatment but that a very striking increase was obtained on all plots receiving nitrogen. The differences between the NP, NK and NPK treatments were small. In general, applications of sulphate of ammonia doubled the yields. Thus these results have substantiated the observation, made on the appearance of the growing crop, that the response to the nitrogenous fertilizer was very marked.

Tissue tests were made only once during the season, over the period July 19-23. As recommended in the method, the petiole of a leaf from the middle of the main stem of tomato plants, and the base of the main stalk of potato plants were used for all the tests. With corn, the nitrate test was applied to the base of the main stem, the phosphate test to the growing tip of the main stalk or the main stalk just below the tassel, and the potassium test to the base of the leaf at the ear node or near the middle of the stalk. Each individual tomato plant was sampled and nitrates were determined on each leaf petiole, but a composite sample from each plot was used for the phosphate and potassium tests. For potatoes and corn, one stalk from each plot was selected and, since there were 8 replicates, this gave 8 stalks from each treatment. The results obtained for each plot, together with the average results for each treatment and the relative yield (check = 100) are presented in Tables 2, 3 and 4 for tomatoes, potatoes, and corn, respectively.

On the tomatoes, the tests showed that nitrates were low in the plants grown on the check and PK treatments, but the levels were raised to medium and high where nitrogen was applied. On the other hand, the

phosphate test, although showing an average value of high and medium for the plants grown on the check and PK treatments, was only medium on the NP and low on the NK and NPK plots. This may have indicated that an insufficient supply of phosphate was available when growth was increased by nitrogen applications. The potassium tests showed satisfactory levels in practically every plant tested.

With the potato crop, the nitrates were low or very low in the plants from the check and PK plots. However, the application of the nitrogenous fertilizer corrected this deficiency and raised the average of the plots to high or very high with only an occasional individual low test. The phosphate tests were very high on the check and PK plots where growth was poor; they gave an average high reading on the NP and NPK plots where good growth was obtained but only a medium average on the NK treatments where no phosphatic fertilizer was added and where growth was also good. The tests for potassium were very high for each individual plant examined.

The nitrates in the corn plants remained low or very low throughout except for an occasional stalk where nitrogen had been applied. Phosphate levels appeared in general to be satisfactory, though a number of low tests were obtained on individual plants on the nitrogen-treated plots where there was increased growth. Potassium was found at an average high level regardless of treatments.

In general, the plant tissue tests have agreed fairly well with the yield results. Nitrates were definitely deficient in the plants grown on the check and the PK-treated plots, but they were increased considerably, when a nitrogenous fertilizer was added, in the tomato and potato plants but not in the corn plants. Apparently the corn crop was still not getting sufficient nitrogen. There was also an indication that more phosphatic fertilizer should have been applied, along with the nitrogen, for the tomato crop.

The results obtained in this preliminary study of the application of Thornton's method of plant tissue testing have been rather interesting and have shown some relationship with the figures for the yields obtained from a number of fertilizer treatments. Considerable variation among individual plants has been shown and this has served to indicate the degree of accuracy that may be expected and has acted as a guide to the general interpretation of results. A sufficient number of plants from each plot should be taken to give an average value to represent that plot. This study has shown that the method has possibilities sufficient to warrant further investigation. It is hoped that this may be carried out in 1944.

TABLE 1.—YIELDS OF TOMATOES, POTATOES AND CORN

Treatment	Yields*		
	Tomatoes	Potatoes	Corn
	lb.	lb.	lb.
Check	22320	6540	4680
PK	22080	6780	4920
NP	53640	14160	11520
NK	61800	14100	10920
NPK	63840	14460	11280

* Yields in lb. per acre.

TABLE 2.—TISSUE TESTS ON INDIVIDUAL PLOTS—TOMATOES

Test	Range and block	Check	PK	NP	NK	NPK
	R5B1	L	L-M	H	L-M	VH
	B2	VL	L	H	M	M-H
NO_3	R6B1	L	L	M	M-H	M-H
	B2	L	L	M-H	H	M-H
	R7B1	L	VL	L	M	M
	B2	L	L-M	H	H	H
	R8B1	L-M	M	M-H	L	L-M
	B2	M	VL	VH	H	VH
	Average test	L	L	H	M	H
	Relative yield	100	99	242	278	287
	R5B1	VH	VH	H	L	L
	B2	M-H	L	L	VH	L
	R6B1	VH	VH	M	L	L
	B2	VH	L-M	L	VL	L
PO_4	R7B1	VH	H	L	L	L
	B2	L-M	L	M	VL	L
	R8B1	VH	VH	M	L	L
	B2	L	L	M	VL	VL
	Average test	H	M	M	L	L
	Relative yield	100	99	242	278	287
	R5B1	VH	VH	VH	VH	VH
	B2	VH	VH	VH	VH	VH
K	R6B1	VH	H	M	VH	H
	B2	M	H	H	H	VH
	R7B1	VH	M	H	VH	VH
	B2	L	L	H	VH	VH
	R8B1	VH	VH	H	VH	VH
	B2	VH	M-H	H	VH	VH
	Average test	H	H	H	VH	VH
	Relative yield	100	99	242	278	287

TABLE 3.—TISSUE TESTS ON INDIVIDUAL PLOTS—POTATOES

Test	Range and block	Check	PK	NP	NK	NPK
	R5B1	L	VL	H	H	H
	B2	VL	VL	VH	VH	VH
NO_3	R6B1	VL	VL	M	H	H
	B2	VL	VL	VH	H	VH
	R7B1	VL	VL	H	L-M	VL
	B2	VL	VL	VH	VH	L-M
	R8B1	VL	VL	VH	H	H
	B2	VH	VL	VH	M	H
	Average test	L	VL	VH	H	H
	Relative yield	100	104	217	216	221
	R5B1	VH	VH	M-H	M	M-H
	B2	H	VH	M-H	M	M-H
PO_4	R6B1	VH	VH	M-H	H	M-H
	B2	VH	H	H	H	M
	R7B1	VH	VH	M	M-H	H
	B2	H	M-H	M	L	H
	R8B1	VH	VH	H	H	H
	B2	M-H	VH	M-H	M	M
	Average test	VH	VH	H	M	H
	Relative yield	100	104	217	216	221

TABLE 3.—TISSUE TESTS ON INDIVIDUAL PLOTS—POTATOES—*Concluded*

Test	Range and block	Check	PK	NP	NK	NPK
	R5B1	VH	VH	VH	VH	VH
	B2	VH	VH	VH	VH	VH
K	R6B1	VH	VH	VH	VH	VH
	B2	VH	VH	VH	VH	VH
	R7B1	VH	VH	VH	VH	VH
	B2	VH	VH	VH	VH	VH
	R8B1	VH	VH	VH	VH	VH
	B2	VH	VH	VH	VH	VH
	Average test	VH	VH	VH	VH	VH
	Relative yield	100	104	217	216	221

TABLE 4.—TISSUE TESTS ON INDIVIDUAL PLOTS—SWEET CORN

Test	Range and block	Check	PK	NP	NK	NPK
	R5B1	VL	VL	L	VL	L-M
	B2	VL	VL	VL	VL	VL
NO_3	R6B1	VL	L	VL	VL	VL
	B2	VL	VL	VL	VL	H
	R7B1	VL	VL	VL	VL	VL
	B2	VL	L	H	H	VL
	R8B1	VL	VL	VL	VL	VL
	B2	L-M	VL	H	VL	H
	Average test	VL	VL	L	VL	L
	Relative yield	100	105	246	233	241
	R5B1	H-VH	H-VH	L	L	L
	B2	VH	H-VH	H-VH	VL	M
PO_4	R6B1	VH	VH	H-VH	L	M-H
	B2	M-H	M	M-H	M-H	H
	R7B1	H	VH	L	L	VH
	B2	H	VH	M	H-VH	H
	R8B1	H	VH	L	H	VH
	B2	VH	H	M-H	H-VH	H-VH
	Average test	H	VH	M	M	H
	Relative yield	100	105	246	233	241
	R5B1	H	H	M	H	H
	B2	H	H	H	VH	M-H
K	R6B1	M	VH	H	H-VH	H-VH
	B2	H	M-H	M-H	H	H
	R7B1	L-M	M	H	M-H	H
	B2	M	H	M	M	VH
	R8B1	VH	VH	VH	VH	H
	B2	M-H	H	M	VH	M
	Average test	H	H	H	H	H
	Relative yield	100	105	246	233	241

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